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CONTENTS

Instructions to Authors. iii

Chase Van Baalen Memorial. ***Patrick Parker and Jack Myers*** viii

Fruits and seeds of *Halophila engelmannii.* ***Calvin McMillan*** 1

The chilling tolerance of black mangrove, *Avicennia germanins*, from the Gulf of Mexico coast of Texas, Louisiana and Florida. ***Calvin McMillan and C. Lee Sherrod*** 9

Isozyme patterns among populations of black mangrove, *Avicennia germinans*, from the Gulf of Mexico-Caribbean and Pacific Panama. ***Calvin McMillan*** 17

Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas.
C. Lee Sherrod, Donald L. Hockaday and Calvin McMillan 27

Changes in chlorophyll *a* concentrations in a shallow water column during a solar eclipse.
Michael Vecchione, Robert Maples and Richard Donahoe 37

Mysidacea from continental shelf water of the north western Gulf of Mexico. ***W. Wayne Price, Andrew P. McAllister, Rae M. Towsley and Marilyn DelRe*** 45

Abundance, age distributions and growth of the Texas hard clam, *Mercenaria mercenaria Texana*, in Texas bays. ***M. Alison Craig and Thomas J. Bright*** 59

Population dynamics of an *R*-selected bivalve, *Mulina Lateralis* (Say) in a North Carolina estuary.
John B. Williams, B.J. Copeland and Robert J. Monroe 73

Movement, growth and survival of spotted seatrout tagged in Bastrop Bayou, Texas.
William B. Baker, Jr., Gary C. Matlock, Lawrence W. McEachron, Albert W. Green and H. E. Hegen 91

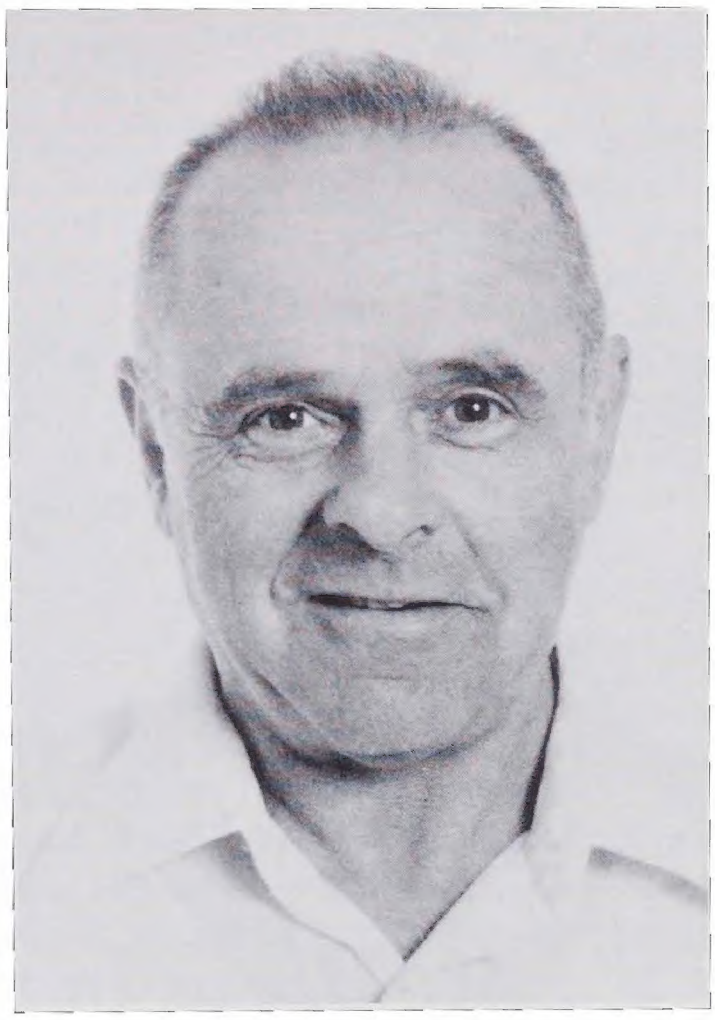
Feeding selectivity and standing stocks of *Fundulus grandis* in an artificial, brackishwater pond, with comments on *Cyprinodon variegatus.*
Peter W. Perschbacher and Kirk Strawn 103

Stable isotope studies on chitin. II. The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in arthropod chitin.
Arndt Schimmelmann and Michael J. DeNiro 113

A stable carbon isotope evaluation of the contribution of terriginous carbon to the marine food web in Bayboro Harbor, Tampa Bay, Florida.
M.E. Conkright and W.M. Sackett 131

Analysis of biological and chemical associations near a turbid coastal front during winter.
Wm. J. Wiseman, Jr, R.E. Turner, F. J. Kelly, L. J. Rouse, Jr., R.F. Shaw 141

Contributions in Marine Science. (1986) Vol. 29:vii–xi.



Chase Van Baalen
1925 - 1986

Professor Chase Van Baalen's contributions to his fellow scientists, students and associates can but slightly be covered in the following memorial notes. The two following notes from colleagues will give a brief glimpse of Chase Van Baalen's broad range as a scientist and as a man.

The first section is by Dr. Jack Myers, Emeritus Professor of Zoology and Botany in Austin of The University of Texas. Professor Myers has been a teacher and research colleague since Chase entered The University of Texas; he was his major professor. They often published together. Chase's last combined research consisted of editorial work on a monographic volume with Dr. Peter Fay. This publication is *Cyanobacteria: Current Research,* published by Elsevier. Chase's chapter in this volume is entitled, *Nitrogenase analyzed reactions: affects of light and* O^2 For this publication, Dr. Jack Myers contributed the biographic memoir notes from Austin, Texas.

The second section is by Professor Patrick L. Parker from The University of Texas at Austin, Marine Science Institute at Port Aransas. Dr. Parker, Professor of Chemistry and Marine Sciences, has been a colleague and "next door" neighbor since they arrived here along the coast in 1961. Dr. Parker notes these reminisces from Port Aransas.

Editor
Donald E. Wohlschlag

* * * * *

Chase Van Baalen - - - From Austin, Texas

Chase Van Baalen died on January 20, 1986, of complications arising from chemotherapy for a lung cancer. He was a Senior Research Scientist in the Marine Science Institute and a Professor of Botany at the University of Texas at Austin. He is survived by his wife Donna, three children, and one grandchild.

Chase is survived also by his scientific family of colleagues and friends. We remember him variously as a convivial drinking buddy, a patient fishing companion, a close-to-the-chest poker player, a quietly competent scientist. In this brief memoir I shall attempt to recount a small sample of Chase's discoveries with something of the flavor of his work and I plead for the pardon of many students and colleagues whose contributions will necessarily go unmentioned. I was a long-time friend, at one time his teacher, in later years his student. Hence this will be a highly personalized account.

Chase once described his undergraduate years as those of a college bum. This must have been too harsh an appraisal because it provided him a broad background, even including field station work on algae and limnology under G.W. Prescott. In 1950, he came to The University of Texas as a graduate student in microbiology under Jackson Foster. In 1954, unhappy with progress toward a Ph.D., he transferred to Zoology to work under me. The move was possible because of Chase's broad biological background but was almost as remarkable as it may seem, especially since it was made amicably to all concerned.

So it was that Chase went to work on the first of the hyperactive blue-greens, *Anacystis nidulans*, then just recently discovered. The problem was to prepare a photochemically active subcellular preparation. He got as far as obtaining high rates of photochemical reduction of indophenol dye. There was a peculiarity that low temperature had to be avoided. In what proved to be an example, often repeated in later years, Chase followed his curiosity: what was bad about low temperature (as 4° C)? He left a cell suspension overnight in the cold room, centrifuged out the cells, and looked at absorption spectra of the supernatant. A component with 270 nm absorption had come out of the cells. All this led to identification and subsequent isolation of several pteridines and, thereafter, several years of fruitful work with the collaboration of our colleague, Hugh Forrest.

In 1959, Chase joined the newly formed Kitchawan Research Laboratory at Ossining, New York. He made the best of an unfavorable situation, profited greatly from occasional contact with Luigi Provasoli, stuck to the character-building task of isolating a collection of 22 marine blue-greens, extended the efficacy of the ASP-2 medium, confirmed a widespread need for vitamin B^{12}. Though published results (*Botanica Marina* 4:129) were not widely appreciated, the experience provided a basis for work for the following 25 years.

In 1961, the timing of a staff vacancy led to an appointment at the Institute of Marine Science in Port Aransas. Here was a special environment, both for blue-green algae and for people. The shallow and productive inland bays

provided a happy home for a wealth of blue-greens in their bottom muds. The sleepy fishing village of Port Aransas became home for Chase, Donna, two children, Patricia and Aaron (with another daughter Julie soon to come). It was a place of beaches, sand, and sun, far removed from the cosmopolitan world.

Most of us engaged in the scientific endeavor take for granted an interdependence among colleagues. This runs from instrumentation to literature review to check-out of new ideas. Self-dependence would impose a scarcely bearable strain. Yet that was the essential feature of the special niche to which Chase adapted. The main university campus at Austin was 200 miles of isolation away. He had to cover the literature by himself, introspectively check out his new ideas, build or repair his own instruments, and solve even trivial logistic problems. One is tempted to suppose that his isolation created a climate of need for invention which nourished his discoveries.

I shall sketchily sample some of his discoveries mainly to show the many facets of his impact upon our understanding of the cyanobacteria.

Requirements for quantitative plating.
Conditions for generating and isolating mutants.
Demonstration of iron acquisition systems.
A poorly utilizable N-source can be used as an internal "chemostat" for growth.
Fructose diphosphate aldolase is indeed a common and required enzyme.
A nickel-requiring *Oscillatoria.*
Ultraviolet killing and photoreactivation.
Ultrastructure of *Trichodesmium* as a key to its fragility.
Marine *Anabaenas* as high-rate N-Fixers.
Isolation of psychrophilic diatoms from Arctic ice.

Many may be critical of my sampling though not of the versatility which it displays.

Chase maintained a healthy skepticism on current dogma. It was a long time before he gave up doubts that phycocyanin has no other photochemical function beyond that of an absorber for harvesting light. In somewhat analogous fashion he had a well-nourished distrust of administrative authority. Through seven directors and eight university presidents he observed that the role of the Institute was seldom understood and that it was generally treated as the University's ugly duckling. Chase's continued fight for academic function of the Institute was not always supported. In contrast he enjoyed the appreciation and support of his scientific colleagues in Austin. And so it should have been, for over a span of 25 years he was the Institute's most productive scientist.

The special niche in which Chase developed naturally changed in the course of time. The village grew up into a city. The blue-green algae became cyanobacteria. And Chase reached out. He attracted and worked side-by-side with students and then gloried in their achievements. He developed effective collaborations on the Austin campus and farther afield in Europe, in India, and in Japan.

A fringe benefit of being a scientist is that one achieves some small measure of immortality. His discoveries became a part of the enduring edifice of science. His students go on to fulfill the example of their mentor. His institution is guided onward in the mold which he helped create. In all these ways the mark of Chase Van Baalen has been deeply etched.

Jack Myers
Professor Emeritus of Zoology and Botany
The University of Texas at Austin
Austin, Texas

*****

Chase Van Baalen - - - From Port Aransas, Texas

Chase Van Baalen died on January 20, 1986 after a short but courageous fight with lung cancer. He was a Senior Research Scientist in the Marine Science Institute and a Professor of Botany and Marine Studies at The University of Texas at Austin. He is survived by his wife Donna, son Aaron, daughters Patricia and Julie and one granddaughter.

Chase joined the Marine Science Institute in the summer of 1961, having been recruited by H. T. Odum to establish a phytoplankton ecology program. Chase did not wander very far into ecology, rather he created, around the blue-green algae, an internationally recognized laboratory for algal physiology. Beginning with essentially a bare room, over 25 years Chase built a sophisticated laboratory. Rita O'Donnell joined the lab very early and helped in many ways, including teaching Chase's graduate students secrets of blue-green culture.

Few scientists have the energy for and devotion to laboratory experimentation that Chase did. He worked in the lab every day, usually all day. That is the way his colleagues and students will remember him. Being there was the way he taught and learned. It may be that the opportunity to work alongside a master is what brought Chase a steady line of students. Eight Ph.D. and seven M.A. students were supervised or co-supervised by him over a period of 22 years.

His interest in the blue-greens led him into a wonderful variety of scientific studies. The early work at Port Aransas dealt with nutrition requirements including vitamin B_{12} nitrogen, phosphorous, and other major elements. Later as his laboratory matured, Chase made discoveries in quantitative surface plating, lipid composition, mutant production, ultraviolet killing and photoreactivation, nitrogen fixation, trace metal nutrition, and the *Trichodesmium* survival problem. Chase participated in several environmental quality

programs that the Institute operated such as the Galveston Bay project, the Bureau of Land Management OCS program, and the Ocean Dumping project. It may be noted that Chase, in the true spirit of science, cooperated with many colleagues in the Institute, in Austin and in the later years, with an international group.

Chase, at home and happy in Port Aransas, accepted and loved the life-style which the area has to offer. He never mentioned the isolation and absence of cultural events. Just as he built scientific gear for his lab, he spent many weekends maintaining his home, cars and his fishing boat. A friendly and helpful companion, a close-to-the-chest poker player, a good citizen, all those describe Chase Van Baalen.

Chase's students will carry on his special traditions and his discoveries will be integrated into the structure of science. His uniqueness as an individual will be remembered by his family, colleagues, and friends, and all others who knew him.

Patrick L. Parker
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FRUITS AND SEEDS OF *HALOPHILA ENGELMANNII* (HYDROCHARITACEAE) IN TEXAS

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ABSTRACT

The fruits and seeds of *Halophila engelmannii* Aschers., a seagrass of the Gulf of Mexico, are reported from Texas and described for the first time. The globose to subglobose fruits, 3.0–5.5 mm in diameter, were commonly produced in May and floated frequently in beach drift in early June. The reticulate testa of the subspherical seeds, 1 mm in diameter, is similar to that reported in the other species, *H. baillonis* Aschers. ex Dickie, in Section Americanae.

INTRODUCTION

The staminate flowers, fruits and seeds of *Halophila engelmannii* Aschers. were unreported at the time den Hartog published *The Sea-Grasses of the World* in 1970. Staminate flowers were reported in Redfish Bay, Texas, in 1972 (McMillan 1974) and were described for the first time by McMillan (1976). Fruits and seeds have remained incompletely described until they were collected in Redfish Bay in 1986 and described in detail for the first time. Although McMillan (1985) reported on frequent production of both staminate and pistillate flowers in late April through mid-June at intervals from 1972 through 1985, the fruits have gone undetected until 1986. In *Halophila*, fruits and seeds are still unreported for *H. hawaiiana* Doty & Stone of the Hawaiian Islands and for *H. johnsonii* Eiseman of Florida and seed for *H. tricostata* Greenway of Australia.

MATERIALS AND METHODS

Collections of *H. engelmannii* were examined in Redfish Bay, Texas, between the cities of Aransas Pass and Port Aransas, at intervals from early March through mid-June of 1986. Weekly monitoring was conducted from mid-May through mid-June along the shallow margins of dredge spoil islands near the junction of the Intracoastal Waterway and the Aransas Channel. Monitoring was conducted in Corpus Christi Bay and in Upper Laguna Madre on 9 June and in Lower Laguna Madre on 17–18 June.

In early March, a demographic evaluation of the *Halophila* population was conducted near the site where staminate flowers have been collected during the period from 1972 to 1985 (McMillan 1974, 1976, 1985). At this Redfish Bay site along the eastern shore of Stedman Island where

numerous patches of *Halophila* were observed in 1985, few remained in 1986. In other areas, dense patches were noted in seagrass beds adjacent to a small spoil island on the western margin of Stedman Island and directly east of the Intracoastal Waterway. The distribution of *Halophila* was in deeper water at the edge of dense beds of *Halodule wrightii* Aschers. that fringe the spoil islands. Although the low tide conditions with clear water in early March allowed a demographic evaluation, subsequent observations were conducted in turbid water on samples that were removed more or less at random from the patches.

The sediment in most *Halophila* sites was composed of very fine particles and was less solid than that of the adjacent *Halodule* beds. The vegetation on the spoil banks adjacent to the *Halodule* area was composed primarily of *Spartina alterniflora* Lois. and *Avicennia germinans* (L.) L.

Voucher specimens of *H. engelmannii* are housed in the Herbarium of the University of Texas at Austin.

RESULTS

Phenology

During May through mid-June, various flowering and fruiting stages were collected in Redfish Bay. On 2 May, both staminate and pistillate flowers were in anthesis and some flowers that were past anthesis had slight swelling of ovaries. On 19 May, staminate and pistillate flowers were in anthesis and fruits with mature seeds were present. On 27 May and again on 3 June, various stages of fruit development were evident along with flowers in

FIG. 1. Flowering and fruiting shoots of *H. engelmannii* collected in Redfish Bay on 3 June 1986. The upper three shoots bear mature or nearly mature fruit still attached to the stems with partial pseudo-whorls of leaves that are highly covered with epiphytes. One spathal bract was removed from center shoot to show shape of fruit. The lower three shoots are left to right: a shoot with a pistillate flower in anthesis; a shoot with a staminate flower in anthesis (and leaves partially cut by herbivore action); a vegetative shoot. Scale at base in mm.

anthesis, both staminate and pistillate (Fig. 1). On 9 June, few staminate and pistillate flowers were in anthesis and some mature fruit was still present, but many stems had old pistillate flowers without developing fruit. On 19 June, only old pistillate flowers without developing fruit were detected in the *Halophila* patches in Redfish Bay.

In Corpus Christi Bay along the shallow shore of Mustang Island, many pistillate and staminate flowers of *Halophila* were observed in early May. At this site in early June, many old pistillate flowers with undeveloped fruits were collected but no pistillate flowers in anthesis or mature fruit were detected in the patches. However, a few ripe fruits still attached to leafy stems were observed in beach drift on Mustang Island.

Numerous fruits were collected in fresh beach drift at the Redfish Bay site on 3, 9, and 19 June. The floating fruits usually had the two subtending spathal bracts still attached at the base, but were mostly devoid of leaves from the pseudo-whorls (Fig. 2). In areas where the drift was lodged between emergent shoots of *Spartina,* the fruits usually floated above the leaves of *Halodule* that were the major ingredient of the drift on 3 June and in a mixture of leaves of *Halodule* and *Thalassia testudinum* Banks ex König on 9 and 19 June. A few fruits of *Halophila* were noted on 27 May in beach drift that consisted primarily of leaves and detached flowers, both staminate and pistillate, of *Thalassia.* The spherical air-filled vesicles of *Sargassum* that are borne on short stalks were common in the drift and strongly resembled the fruit of *Halophila* in size and shape.

FIG. 2. Fruits collected in beach drift on a dredge spoil island in Redfish Bay on 3 June 1986. Spathal bracts are still attached to fruits along with various amounts of stem. One bract on each of the two fruits on the right has been broken. Scale at base in mm.

On 9 June, numerous fruits were collected in fresh beach drift on the western shore of Upper Laguna Madre near the Intracoastal Waterway passage into Corpus Christi Bay. Although no patches of *Halophila* were observed in the immediate vicinity of the beach drift, *Halophila* has been reported in Upper Laguna Madre (Merkord 1978).

On 17–18 June, no fruits were observed in beach drift in Lower Laguna Madre, but some old pistillate flowers without developing fruit were detected in samples from *Halophila* patches on the western side near Port Isabel and on the eastern side at South Padre Island.

Fruit

The mean size of the fruit showed an increase during late May and early June (Table 1). Among 20 of the largest fruits in each collection, the mean showed an increase from 3.5 mm on 19 May to 4.5 mm in beach drift on 3 June. The largest fruits were 4.0 mm in diameter on 19 May, but fruits measuring 5.5 mm in diameter were collected in beach drift on 3 June.

The fruits ranged in shape from globose to subglobose. In the beach drift collected on 3 June, one-third of the fruits were globose and the remainder subglobose. The widest dimension of the fruit was in the direction of the two subtending spathal bracts and the narrowest was at right angles to the bracts.

TABLE 1.

Measurements of fruits of *Halophila engelmannii* in Texas[1]

Date of Collection	Site of Collection	Fruit diameter (mm)[2] Range	Mean	Stylar beak length (mm) Range	Mean
Redfish Bay					
19 May	patches	3.0-4.0	3.5	3.5-6.0	5.0
27 May	patches	3.3-4.5	3.9	4.0-5.5	4.6
3 June	patches	3.6-5.0	4.2	4.0-6.0	4.8
	drift	3.8-5.5	4.5	3.0-6.0	5.1
9 June	patches	3.0-4.2	3.5	4.0-6.0	4.4
	drift	3.5-4.5	4.0	4.0-6.0	5.2
19 June	drift	3.5-4.6	4.0	4.0-6.0	4.6
Upper Laguna Madre					
9 June	drift	3.0-4.5	3.6	4.0-6.0	4.7

[1] Twenty of the largest fruits were measured for each collection.

[2] The diameter is for the widest portion of the fruit. Many of the fruits were subglobose with the widest demension in the direction of the two subtending spathal bracts. The narrower dimension of the fruit was 0.1 to 1.0 mm less (mean 0.4 mm) than the wider dimension on 3 June.

Among the subglobose fruits, the difference between the two dimensions varied from 0.1 to 1.0 mm, with a mean of 0.4 mm.

The stylar beak of the fruit showed a range of variation that was not correlated with the date of collection (Table 1). Some of the longest beaks, 6.0 mm, were collected on each date except 27 May. The mean lengths ranged from 4.4 to 5.2 mm among the various collections.

The fleshy-walled capsule remained green while attached to the stem in the patches and either attached or unattached to portions of the stem in the drift (Fig. 2). The pericarp is membranous and the endocarp is fleshy.

Fruits from the beach drift collections of 3, 9 and 19 June were floated in artificial seawater (Instant Ocean, 35‰) in the laboratory to determine the nature of fruit opening. The green capsule ruptured and the fruit wall split roughly along 3 lines (Fig. 3). As the wall folded back toward the stylar beak, the seeds were expelled. The fruit wall dropped out of the water column, but the seeds floated on the water surface. The seeds floated even if the water was agitated but immediately sank if they were pushed below the water surface.

Seed

The number of seeds per fruit varied from 1 to 20, with a mean of 10. Although most of the fruits collected on 27 May had 7 or more seeds (mean of 12), one small fruit contained only one mature seed along with several

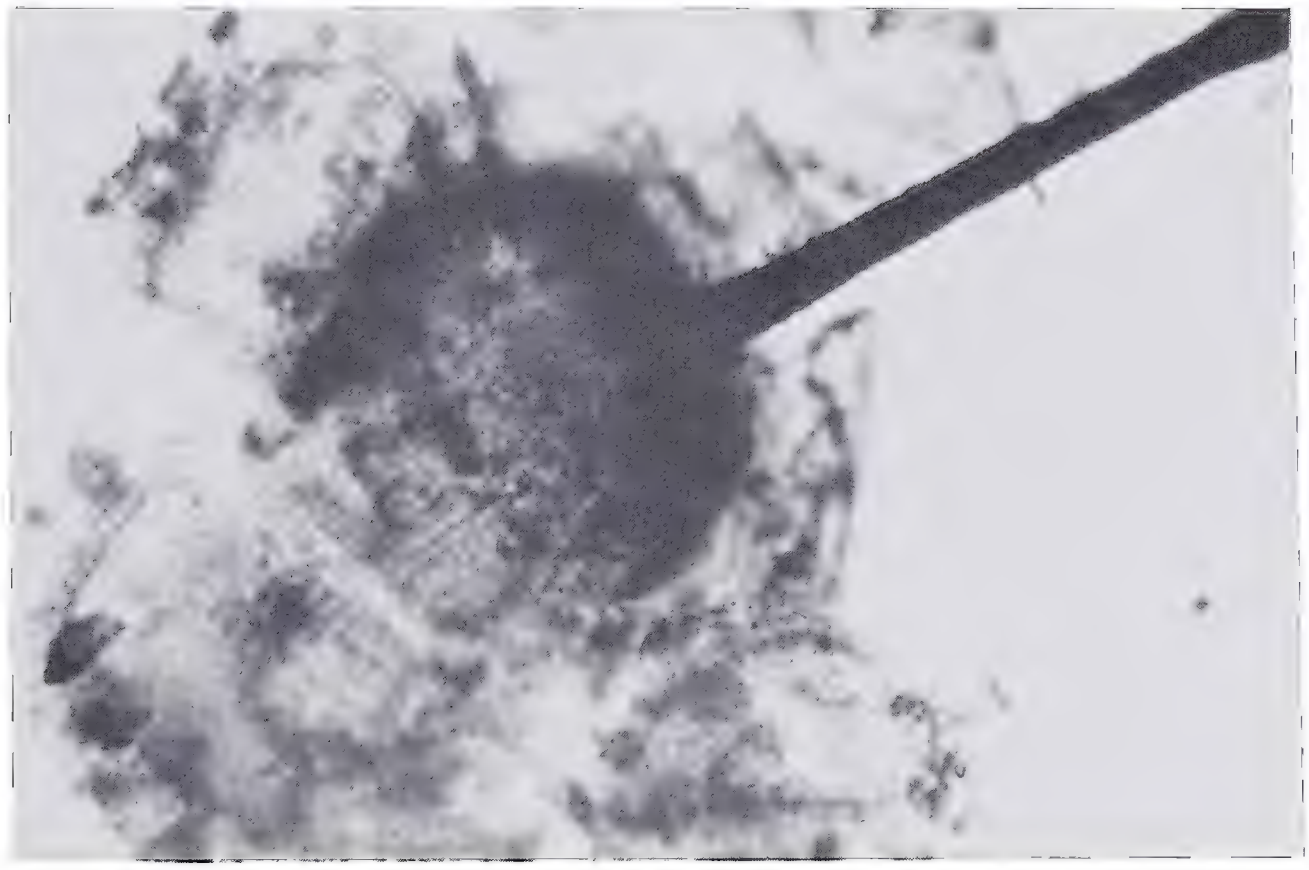

FIG. 3. Capsule after the release of seeds from the fruit. The fruit wall has split roughly along three lines and curled toward the stylar beak. The cap of the fruit remains unsplit adjacent to the beak at the upper right. Beak is *ca.* 5 mm long.

undeveloped ovules and four other small fruits contained only 3 or 4 mature seeds. Most fruits with less than 20 seeds contained undeveloped ovules.

The seeds are subspherical, apiculate at both ends, and *ca.* 1 mm in diameter (Fig. 4). The testa is reticulate. Some mature seeds were sieved out of the sediment in the *Halophila* patches. Both the extent of the seed reserve in the sediments and the germination of seeds are under investigation.

DISCUSSION

Although den Hartog (1970) gave no description of fruits and seeds of *H. engelmannii*, he reported details for the other species, *H. baillonis* Aschers. ex Dickie, in Section Americanae. He described the fruit of *H. baillonis* as globular, 1–2 mm in diameter, with a stylar beak, 4–5 mm long. He described the fruit wall as membranaceous and the endocarp as fleshy. The seeds of *H. baillonis* were described as 10–20 per fruit and subspherical, apiculate at both ends. Although he did not give a seed diameter, he reported the testa to be reticulate.

The above descriptions of fruits and seeds of *H. baillonis* are very similar to those given above for *H. engelmannii.* The diameter of the fruit of *H. engelmannii* is greater, 3.0–5.5 mm, but the number of seeds per fruit may be approximately the same, indicating that the seed size of *H. baillonis* may be less than the 1 mm in diameter given for *H. engelmannii.*

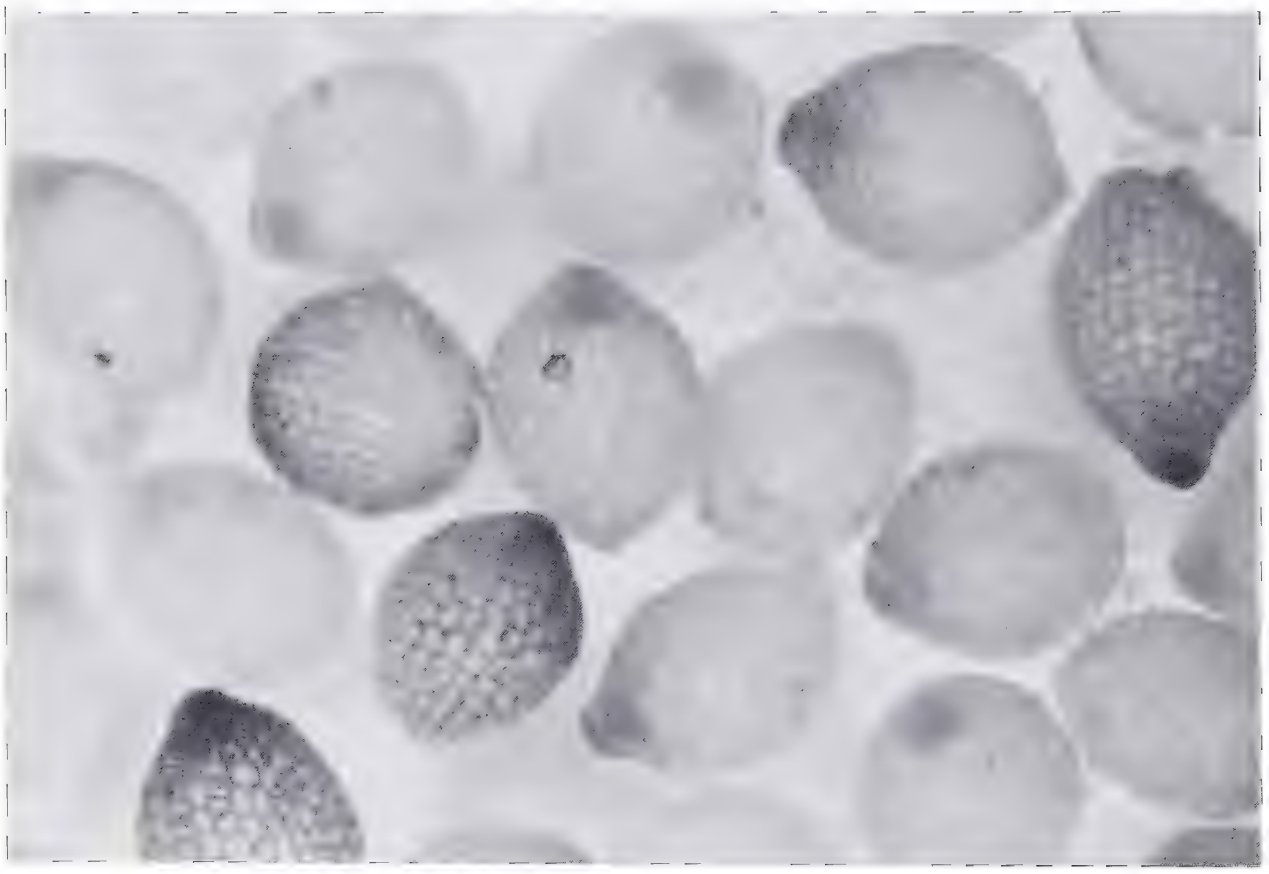

FIG. 4. Subspherical seeds of *H. engelmannii.* The reticulum varied from white to brown among the recently released seeds, but the majority of the seeds were white. The diameter is *ca.* 1 mm.

In Section Americanae, there has been confusion concerning the application of *H. baillonis*, as well as the description of its fruits and seeds. Den Hartog (1970) applied the name to plants of the Caribbean (and the Pacific Coast of Panama) with a pseudo-whorl of leaves that is also characteristic of *H. engelmannii* of the Gulf of Mexico. Other authors have applied *H. baillonis* to a species in Section Halophila.

Illustrations of flowers and fruits that accompany *Halophila* in Small (1933) reflect some of the taxonomic problems in the genus. In his descriptions, Small has applied *H. baillonis* to plants that are referred to *H. decipiens* Ostenfeld by den Hartog (1970). Although Small does not indicate which of the Florida species is illustrated, it is clear that the flowers, both staminate and pistillate in the same spathe, and the fruit with a short stylar beak refer to his *H. baillonis (H. decipiens)*. Small describes the fruit of *H. engelmannii* as 2.5–3.0 mm long and ovoid or globose-ovoid, but does not include it with the illustrations.

The fruit of *H. engelmannii* is described variously in recent taxonomic reports. Correll and Correll (1972) described it as a "membranous capsule with 3 parietal placentae, enclosed in the sheath; seeds numerous," and repeated this description in a recent flora of the Bahamas (Correll and Correll 1982). Godfrey and Wooten (1979) described the fruit as "an ovoid capsule containing many seeds." The above description by Correll and Correll (1972) originally appeared in the *Manual of the Vascular Plants of Texas* by Correll and Johnston (1970) and may have been based on pistillate flowers that were in the Lundell Herbarium (now housed in the Herbarium of the University of Texas at Austin) but not on mature fruit.

In *Halophila,* the details of flowers, fruits and/or seeds are still not available for some species and from some areas. The staminate flower of *H. engelmannii* was not reported for Florida until 1982 (Short and Cambridge 1984) and the fruit may still be unreported for Florida. Herbert (1986) has described the staminate flower for *H. hawaiiana*, but the fruits and seeds for this species are still unreported. Eiseman and McMillan (1980) reported a new species, *H. johnsonii*, from the Atlantic Coast of Florida, but did not have material for a description of the staminate flower or for fruit and seeds. Greenway (1979) described a new species, *H. tricostata,* from the Great Barrier Reef of Australia but did not have material for describing mature seeds. Eiseman and McMillan (1980) considered the possibility that apomictic reproduction might characterize *H. engelmannii, H. hawaiiana* and *H. johnsonii*, but the likelihood of this type of reproduction is diminished with the collection of staminate flowers, fruits and seeds for *H. engelmannii* and of staminate flowers for *H. hawaiiana.*

Although observations have been made in Redfish Bay at intervals from 1961 through 1985 (McMillan 1985, unpublished data 1961–1971), it is difficult to explain why 1986 is the first year in which fruits of *H. engelmannii* have been collected. Collections in other years in mid-May did not contain fruits in various stages of development as were present in 1986. An earlier phenological pattern in 1986 may have resulted from the unusually mild winter of 1985–1986, with no temperatures below 0° C being recorded from

coastal sites to inland Central Texas in January and continuous mild conditions of February and March. Although the collections in 1986 were taken in Redfish Bay from a different site from that studied in 1961–1985 and may indicate that site-oriented conditions may be involved in sexual reproduction of *Halophila*, the collection of mature fruit in Corpus Christi Bay and in Upper Laguna Madre indicates the widespread production of fruit by *H. engelmannii* in 1986.

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LITERATURE CITED

CORRELL, D.S. AND H.B. CORRELL. 1972. *Aquatic and Wetland Plants of Southwestern United States.* U.S. Government Printing Office, Washington, D.C. 1777 p.

_____ and _____. 1982. *Flora of the Bahama Archipelago.* J. Cramer, Vaduz. 1692 p.

_____ and M.C. JOHNSTON. 1970. *Manual of the Vascular Plants of Texas.* Texas Research Foundation, Renner, Texas. 1881 p.

den HARTOG, C. 1970. *The Sea-Grasses of the World.* North Holland, Amsterdam. 275 p.

EISEMAN, N.J. and C. McMILLAN. 1980. A new species of seagrass, *Halophila johnsonii*, from the Atlantic coast of Florida. *Aquatic Botany.* 9:15–19.

GODFREY, R.K. and J.M. WOOTEN. 1979. *Aquatic and Wetland Plants of Southeastern United States.* University of Georgia Press, Athens, Georgia. 261 p.

GREENWAY, M. 1979. *Halophila tricostata* (Hydrocharitaceae), a new species of seagrass from the Great Barrier Reef region. *Aquatic Botany.* 7:67–70.

HERBERT, D.A. 1986. Staminate flowers of *Halophila hawaiiana*: description and notes on its flowering ecology. *Aquatic Botany.* (in press).

McMILLAN, C. 1974. Salt tolerance of mangroves and submerged aquatic plants. In: R.J. Reimold and W.H. Queen (eds.) *Ecology of Halophytes.* pp. 379–390. Academic Press. New York, New York.

_____. 1976. Experimental studies on flowering and reproduction in seagrasses. *Aquatic Botany.* 2:87–92.

_____. 1985. Staminate flowers and reproductive physiology of *Halophila engelmanni. Contributions in Marine Science.* 28:151–159.

MERKORD, G.W. 1978. The distribution and abundance of seagrasses in Laguna Madre of Texas. M.S. Thesis. Texas A&I University, Kingsville, Texas. 56 pp.

SHORT, F.T. and M.L. CAMBRIDGE. 1984. Male flowers of *Halophila engelmanni*: description and flowering ecology. *Aquatic Botany.* 18: 413–415.

SMALL, J.K. 1933. *Manual of the Southeastern Flora.* University of North Carolina Press, Chapel Hill, North Carolina. 1554 pp.

Contributions in Marine Science. (1986) Vol. 29:9–16.

THE CHILLING TOLERANCE OF BLACK MANGROVE, *AVICENNIA GERMINANS*, FROM THE GULF OF MEXICO COAST OF TEXAS, LOUISIANA AND FLORIDA

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ABSTRACT

Seedling populations of *Avicennia germinans* (L.) L. from the Gulf of Mexico coast of Texas, Louisiana and Florida showed various amounts of physiological dysfunction and injury after exposure to chilling temperatures of 2–3° C. Although all of the plants had greater chill tolerance than has been shown for plants of more tropical origin in the Gulf-Caribbean, those of Texas were more tolerant to extended chilling conditions than those of Louisiana and Florida. Populations from diverse sites in Texas from the northernmost distribution at Galveston Island to the Rio Grande were not strongly differentiated in chilling tolerances. The recurrent pattern of low winter temperature in the northern Gulf of Mexico has selected chilling tolerant populations, but those of the western side show the least physiological dysfunction and injury from chilling temperatures.

INTRODUCTION

A gradient of chilling tolerance has been demonstrated in black mangrove, *Avicennia germinans* (L.) L., from the Gulf of Mexico-Caribbean (McMillan 1975; Markley, McMillan and Thompson 1982) with plants originating in more temperate sites showing the greatest chilling tolerance and those from more tropical sites having less tolerance. The mangrove populations that have been studied extend south from the central Texas coast at Harbor Island and from the southern Florida coast at Miami (Fig.1). To explore the comparative tolerances to chilling among populations of the northern Gulf of Mexico, plants from diverse sites in Texas, Louisiana and Florida were grown under controlled conditions and subjected to experimental chilling at 2–3° C.

Many tropical and subtropical plants show physiological dysfunction and chilling injury after exposure to temperatures above freezing. The phenome-

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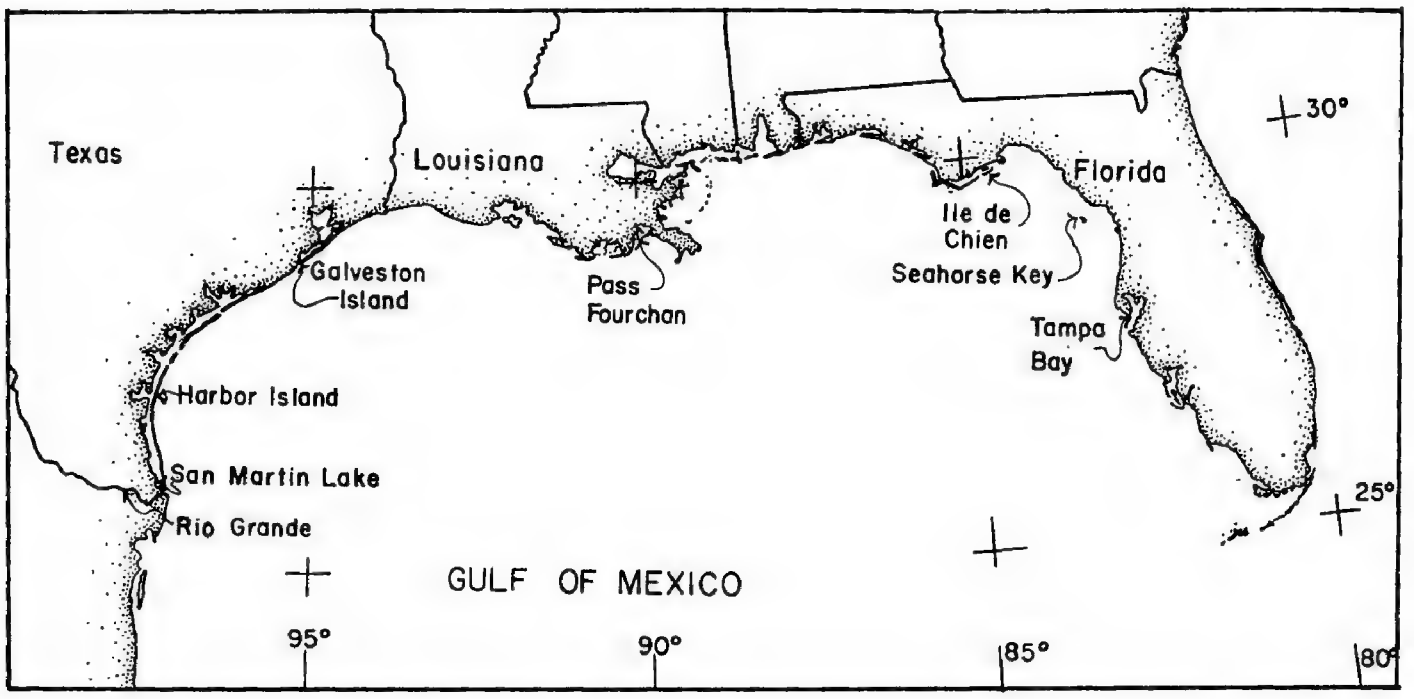

FIG. 1. Map of the northern Gulf of Mexico showing collection sites for black mangrove. Although black mangroves have been reported from the northern Florida coast at Ile de Chien, this population was not included in the chilling comparison.

non has been well documented in agricultural crop plants (Lyons, Graham and Raison 1979a) and plant sensitivity to low temperatures has been recorded for centuries. Few species except mangroves and seagrasses are distributed from the tropics into temperate coastlines. In each seagrass species from the Gulf of Mexico-Caribbean, *Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kutz. and *Halodule wrightii* Aschers. (McMillan 1979) and in each mangrove species from the same region, *A. germinans, Rhizophora mangle* L. (red mangrove) and *Laguncularia racemosa* (L.) Gaertn. (white mangrove) (Markley *et al.* 1982), populations of more tropical origin showed the most chilling injury. Although the mechanism involved in chilling sensitivity has not been well understood, the reviews of chilling injury in plants (Lyons 1973, Lyons *et al.* 1979a, Graham and Patterson 1982) have examined some of the manifestations of chilling injury and have discussed a number of proposals to accommodate the physiological and biochemical changes associated with chilling effects. Recently Norman, McMillan and Thompson (1984) associated chilling sensitivity in *A. germinans* with the fatty acid and molecular species composition of phosphatidylglycerols.

MATERIALS AND METHODS

Propagules produced in 1982 and/or established seedlings, *ca.* 1-year old, were collected in 1982–83 at diverse sites (Fig. 1) along the northern coast of the Gulf of Mexico. In Texas, propagules were collected at the mouth of the Rio Grande (from the tallest mangroves in Texas) (Sherrod, unpublished data 1982) and at San Martin Lake along the Brownsville Ship Channel, Cameron County; at Harbor Island, Nueces County; and at Galveston Island, Galveston County. In Louisiana, both propagules and established seedlings were collected at Pass Fourchon, Lafourche Parish. In Florida, propagules were collected at Seahorse Key, Levy County, and established seedlings at Tampa Bay, Hillsborough County. For the two sites in Cameron County,

Texas, three seedling progenies for each were used in the comparison, but for the other sites, the seedlings represented a mixture of progenies.

The propagules were floated in 3.6-L tubs of loam and tap water under growth chamber conditions (30° C day/24° C night) until they had produced roots and shoots. The seedlings were then planted individually in 500-ml plastic cups filled with fine sandy loam of Central Texas origin and watered with tapwater. Subsequently the seedlings received additions of artificial seawater (Instant Ocean) and Miracle-Gro at intervals.

Before the chilling tests of 1983–1984, the plants were kept in growth chambers at 24° C at 14 h day lengths. They were moved directly to a cold room that was kept constantly at the chilling temperatures of 2–3° C (12 h light and 12 h dark). After chilling, the plants were returned to the 24° C conditions and monitored for dysfunction, injury and survival. Some seedlings were kept at 18° C prior to chilling to assess possible effects of temperature pre-conditioning and hardening. Five seedlings for a collection site or individual progeny were included in most of the chilling tests. Seedlings grown from field-collected propagules were 6–8 months from rooting at the beginning of the tests and those that had rooted in the field were approximately 15–20 cm in height.

The definition of chilling injury (damage to plant tissue, cells or organs which result from the imposition of low temperature, *i.e.*, chilling or chilling treatment, for a period of time sufficient to cause permanent or irreversible damage) and of dysfunction (a disordered or impaired function in response to temperature which if allowed to occur for sufficient time, will cause an injury) follow those of Lyons, Raison and Steponkus (1979b). Chilling involves the exposure of plant material to some low temperature above freezing.

RESULTS

The initial testing of chilling tolerances compared seedlings from the mouth of the Rio Grande, TX; Seahorse Key, FL; and Pass Fourchon, LA. In a 24 h comparison at 2–3° C, 40% of the Seahorse Key seedlings showed a slight physiological dysfunction with the bending of the stem apex and a wilted appearance, but the seedlings from the Rio Grande and from Pass Fourchon showed no dysfunction. After four days at 24° C, the Seahorse Key seedlings had recovered and were no longer showing dysfunction symptoms.

Additional seedlings from Seahorse Key were then subjected to 5 days at 2–3° C, along with seedlings from the Rio Grande and Pass Fourchon. When they were removed from the chilling conditions, 20% of the Pass Fourchon seedlings, 40% of the Rio Grande and 60% of the Seahorse Key showed dysfunction (wilting of apical leaves). After 1 day at 24° C, all of the Seahorse Key seedlings showed injury to the stems below the apical leaves, but all Pass Fourchon and Rio Grande seedlings showed only wilting of the stems. During the subsequent 30-day observation period, all of the Seahorse Key seedlings progressively showed more injury but with only some green tissue remaining in the cotyledons and all subsequently died. For the Pass Fourchon seedlings, 1 died and 2 continued to show slight dysfunction during the 30-day observation, but 4 of the 5 seedlings fully recovered during an additional 14-day period. For the Rio Grande seedlings, 6 showed stem bending during the 30-day observation, but all 10 fully recovered with erect stems after the additional 14-day period.

All of the Gulf of Mexico seedling populations were then compared under chilling conditions for 3 and 4 days (Table 1). In the 3-day chilling test, the

TABLE 1

Comparison of chilling tolerances of *Avicennia germinans* from the Gulf of Mexico.

Collection Site	Latitude (N)	Percentage of Seedlings with Physiological Dysfunction (DY), Injury (IN) and Survival (S) after 3 days at 2-3°C			4 days at 2-3°C		
		DY	IN	S	DY	IN	S
Texas							
Galveston Island	29° 20'	0	0	100	20	20	100
Harbor Island	27° 45'	0	0	100	0	0	100
San Martin Lake	26°	20	0	100	47	0	100
Mouth of the Rio Grande	25° 55'	33	20	100	80	60	100
Louisiana							
Pass Fourchan	29° 15'	40	30	100	40	40	60
Florida							
Seahorse Key	29° 8'	80	80	100	60	60	40
Tampa Bay	27° 45'	20	20	100	60	60	40

[a] 5 seedlings were tested for Galveston Island, Harbor Island, Seahorse Key and Tampa Bay in each chilling comparison, 10 seedlings (5 laboratory-germinated, 5 field established) for Pass Fourchan and 15 seedlings (5 for each of 3 progenies) for San Martin Lake and Mouth of the Rio Grande (only 1 seedling progeny for Rio Grande in 4-day test).

least dysfunction and injury was shown by Texas plants and the most injury by plants of Seahorse Key, Florida. Under the 4-day chilling, most seedling populations showed more dysfunction than during the shorter chilling treatment, but the death of seedlings during subsequent observation occurred only in the Louisiana and Florida material. The responses of transplanted seedlings and those rooted in the laboratory from Louisiana were similar.

In both the 3- and 4-day chilling tests (Table 1), the seedlings from the mouth of the Rio Grande showed more sensitivity to chilling than that shown by plants from the San Martin Lake site. The differences in percentages of dysfunction and injury for the 4-day treatment may reflect the use of only 1 seedling progeny for the Rio Grande population and 3 for the San Martin Lake population.

To examine the possibility that pre-conditioning or hardening at cool temperatures might affect the response of black mangrove seedlings to chilling conditions, the various populations were kept at 18° C before being subjected to chilling at 2–3° C. An initial 3-day chill test included plants from

Harbor Island and the mouth of the Rio Grande, TX; and Pass Fourchon, LA. No dysfunction was noted for seedlings from Harbor Island or Pass Fourchon, but 20% of the Rio Grande seedlings had wilting of the apical leaves. All of these seedlings showed rapid recovery and after 24 h at 24° C showed no dysfunction symptoms. Among seedlings without the pre-treatment at 18° C (Table 1), 60% of the Harbor Island plants showed slight dysfunction after 3 days at 2–3° C and injury was recorded among the seedlings from the Rio Grande and Pass Fourchon.

In duplicate tests after pre-conditioning at 18° C, all of the populations showed some dysfunction after chilling for 5 days (Table 2), but all of the plants survived. Without the pre-conditioning, all of the populations showed a greater percentage of dysfunction and some of the seedlings from Pass Fourchon and Seahorse Key failed to survive.

TABLE 2

Comparison of *Avicennia germinans* from the Gulf of Mexico after 5 days at chilling at 2–3° C.

Collection Site	Percentage of Seedlings with Physiological Dysfunction (DY) and Survival (S) With and Without Pre-Conditioning for 3 Weeks at 18° C			
	With Preconditiong[a]		Without Preconditiong[b]	
	DY	S	DY	S
Texas				
Galveston Island	60	100	100	100
Harbor Island	10	100	60	100
San Martin Lake	54	100	100	100
Mouth of the Rio Grande	56	100	100	100
Louisiana				
Pass Fourchan	37	100	100	80
Florida				
Seahorse Key	80	100	100	60
Tampa Bay	30	100	-	-

[a] Duplicate tests were conducted with pre-conditioning at 18° C. Percentages are means of the tests.

[b] The San Martin and Mouth of the Rio Grande populations were represented by 15 seedlings each, Louisiana population by 10 seedlings, and the other populations by 5 seedlings.

For a further comparison of plants from Harbor Island and from Tampa Bay, both sites at comparable latitudes, seedlings without pre-conditioning at 18° C were tested for survival after 5 days at 2–3° C. Among the Harbor Island seedlings, only 1 of 18 plants failed to survive, but among those from Tampa Bay, only 1 of 17 survived the extended chilling.

DISCUSSION

The comparative testing of seedlings of black mangrove from the northern Gulf of Mexico indicates that Texas seedlings have less sensitivity to chilling temperatures of 2–3° C than do seedlings originating in Louisiana and Florida. Although the temperature conditions under which the seedlings are grown prior to the exposure to chilling affects the percentage of physiological dysfunction, injury and survival among the populations, those from Texas consistently showed the least damaging effects of chilling conditions.

Although the Louisiana black mangrove population at Pass Fourchon is among the northernmost in the Gulf of Mexico, occurring at a comparable latitude to that of the mangroves on Galveston Island and Seahorse Key, the responses to chilling were more like those of the Florida coast. Consistently, the Louisiana plants, both the laboratory-germinated seedlings and those transplanted as established seedlings, showed less survival after chilling than was shown for the Texas populations.

Among the Texas populations, the greater height of plants at the mouth of the Rio Grande led to the possibility that they might be of more tropical origin than the usual shorter plants typical at San Martin Lake (Sherrod and McMillan 1981). For this comparison of chilling tolerance, the seeds of three different trees at each of the two sites, mouth of the Rio Grande and San Martin Lake, were used to determine if the Rio Grande plants had the chill tolerance shown by plants of more tropical origin in Mexico (Markley *et al.* 1982). While there was no clear separation of the plants from the two sites in their over-all sensitivity to chilling, those of the Rio Grande site showed slightly greater sensitivity but not of the degree typical of Mexico plants. The difference in stature of the two populations probably results largely from their immediate habitat differences, one being adjacent to a freshwater source and the other being consistently in a hypersaline situation.

The black mangrove populations of the Gulf of Mexico-Caribbean have shown a divergence in their isozyme patterning (McMillan 1986). Populations from the western side in Texas and Mexico show different isozyme patterning for phosphoglucose mutase and phosphoglucose isomerase than indicated for plants of Miami, the Florida Keys, St. Croix and Jamaica. Sherrod and McMillan (1985) have suggested that the divergence resulted from the post-Pleistocene recolonization of the shores of the Gulf of Mexico and that the latitudinal variation in chilling tolerance developed through natural selection of latitudinal adaptive gradients. Although the isozyme patterns have not been studied for plants of Louisiana and those from Seahorse Key and Tampa Bay in Florida, it is possible that those of the Florida sites represent the eastern

pattern shown by Miami plants. The geographically intermediate site in Louisiana makes it more difficult to speculate on its origin, but the greater similarity of chilling tolerance of Louisiana and Florida plants might indicate that the Louisiana plants represent an extension from Florida or a mixture of western and eastern plants. The recent discovery of black mangrove at Ile de Chien, west of Apalachee Bay (Johnston, S.A., personal communication 1981) represents a geographically intermediate site between Seahorse Key and Louisiana.

Although few other plants of the Gulf of Mexico have been compared for chilling tolerances, the seagrasses, as indicated above, were studied by McMillan (1979). In *Thalassia testudinum* (turtle grass), *Halodule wrightii* (shoal grass) and *Syringodium filiforme* (manatee grass), greater chilling tolerance was shown by plants of the Texas coast (Redfish Bay and Lower Laguna Madre, adjacent to Harbor Island and the San Martin Lake mangrove sites, respectively) than for those of either Tampa Bay or Biscayne Bay near Miami. Seagrasses of the Louisiana coast (Chanteleur Islands) and those of the northern Florida coast at Apalachee Bay showed chilling tolerances that were similar to those of Texas plants. Although the black mangroves of the Apalachee Bay area (Ile de Chien, as indicated above) have not been tested for chilling tolerances, those of Louisiana were more like those of Florida in their tolerances.

The differences in chilling tolerances among the black mangrove populations may reflect the influences of the winter temperature patterns of the northern Gulf of Mexico. The northern cold fronts approach the Texas coast from inland with only slight moderation of temperature, but the fronts usually approach the Florida coast by an east by southeasterly direction over the Gulf with a moderating effect. Although the black mangroves at Harbor Island, Texas, and at Tampa Bay, Florida, are at comparable latitudes, the differences in chilling tolerance may reflect the localized adaptation to longer periods at chilling temperatures in Texas. The inadequacy of climatic information for each of the mangrove collection sites, however, does not permit a determination of the actual differences in chilling conditions among the sites.

Although chilling temperatures of 2–3° C are recurrent in the winters along the coast of the northern Gulf of Mexico, extended periods of subfreezing conditions are occasionally reported with severe destruction in mangrove populations. The subfreezing temperatures in December, 1983 caused an estimated 80 to 85 percent mortality in Texas mangrove populations (Sherrod and McMillan 1985). Similar freeze effects have been noted in Florida (Davis 1940) and for Seahorse Key (Lugo and Zucca 1977) and in Louisiana (West 1977). The frequency, duration, and/or severity of freezing temperatures is a prime factor governing the distribution and abundance of black mangroves in the extreme northern Gulf of Mexico.

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LITERATURE CITED

DAVIS, J.H. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Institute of Washington Publication 517. *Papers of the Tortuga Laboratory.* 32:303–412.

GRAHAM, D. and D.B. PATTERSON. 1982. Responses of plants to low, non-freezing temperature: proteins, metabolism and acclimation. *Annual Reviews of Plant Physiology.* 33:347–372.

LUGO, A.E. and G.P. ZUCCA. 1977. The impact of low temperature stress on mangrove structure and growth. *Tropical Ecology.* 18:149–161.

LYONS, J.M. 1973. Chilling injury in plants. *Annual Reviews of Plant Physiology.* 24:445–466.

_____, D. GRAHAM and J.K. RAISON. 1979a. *Low temperature stress in crop plants: the role of the membrane.* Academic Press, New York.

_____, J.K. RAISON and P.L. STEPONKUS. 1979b. The plant membrane in response to low temperature: an overview. pp. 1–24. In J.M. Lyons, D. Graham, and J.K. Raison (eds.) *Low temperature stress in crop plants: the role of the membrane.* Academic Press, New York.

MARKLEY, J.L., C. McMILLAN and G.A. THOMPSON. 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle,* from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany.* 60:2704–2715.

McMILLAN, C. 1975. Adaptive differentiation to chilling in mangrove populations. pp. 62–68. In G.E. Walsh, S.C. Snedaker and H.J. Teas (eds.) *Proceedings of the International Symposium on Biology and Management of Mangroves.* Vol. 1. University of Florida, Gainesville.

_____. 1979. Differentiation in response to chilling temperatures among populations of three marine spermatophytes, *Thalassia testudinum, Syringodium filiforme* and *Halodule wrightii. American Journal of Botany.* 66:810–819.

_____. 1986. Isozyme patterns among populations of black mangrove, *Avicennia germinans,* from the Gulf of Mexico-Caribbean and Pacific Panama. *Contributions in Marine Science.* 29:000–000.

NORMAN, H.A., C. McMILLAN and G.A. THOMPSON. 1984. Phosphatidylglycerol molecular species in chilling-sensitive and chilling-resistant populations of *Avicennia germinans* (L.) L. *Plant and Cell Physiology.* 25:1437–1444.

SHERROD, C.L. and C. McMILLAN. 1981. Black mangrove, *Avicennia germinans,* in Texas: past and present distribution. *Contributions in Marine Science.* 24:115–131.

_____ and C. McMILLAN. 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science.* 28:129–140.

WEST, R.C. 1977. Tidal salt-marsh and mangal formations of middle and South America. pp. 193–213. In V.J. Chapman (ed.) *Ecosystems of the World I: Wet Coastal Ecosystems.* Elsevier Scientific Publishing Co., New York.

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ISOZYME PATTERNS AMONG POPULATIONS OF BLACK MANGROVE, *AVICENNIA GERMINANS*, FROM THE GULF OF MEXICO-CARIBBEAN AND PACIFIC PANAMA

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ABSTRACT

Among laboratory-germinated plants of black mangrove, *Avicennia germinans* (L.) L., populations showed a divergence in isozyme patterning between the eastern and western sides of the Gulf of Mexico-Caribbean. Populations from the western side in Texas and Mexico showed patterns for phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI) that were different from those of populations on the eastern side in Florida, Jamaica and St. Croix, U.S. Virgin Islands. Populations from Central America in Belize and Caribbean Panama showed a mixture of patterns for PGM and the eastern pattern for PGI. Some plants (*A. germinans*) in a mixed population from Pacific Panama differed in their patterns of PGI from plants of the Gulf-Caribbean and others (in *A. bicolor* Standl.) differed in most enzyme systems from those of *A. germinans*. Although the taxonomy of *Avicennia* is unsettled, the populations that diverge isozymally along the eastern and western sides of the Gulf-Caribbean are generally recognized in *A. germinans*.

INTRODUCTION

The mangroves have extended their distributions from tropical sites in the Caribbean to more temperate sites in the Gulf of Mexico through the natural selection of ecotypic variants that are more tolerant of chilling temperatures (Markley, McMillan and Thompson 1982). Although *Avicennia germinans* (L.) L., black mangrove; *Rhizophora mangle* L., red mangrove; *Laguncularia racemosa* (L.) Gaertn., white mangrove; and *Conocarpus erectus* L., button mangrove, extend northward in Mexico to near 24° N lat. (Lot-Helgueras, Vasquez-Yanes and Menendez 1975; McMillan, unpublished data 1975–76), only *A. germinans* continues to *ca.* 29° N lat. in Texas (Sherrod and McMillan 1981) and Louisiana. On the eastern side of the Gulf, the mangroves have

extended northward to Cedar Key at *ca.* 29° N lat. (Davis 1940, Lugo and Zucca 1977), but only the black mangrove has extended northward to Ile de Chien, west of Apalachee Bay (Johnston, S.A., personal communication 1981) at near 30° N lat. Sherrod and McMillan (1985) have noted that the apparent Pleistocene extirpation of mangroves from the northern Gulf and the post-Pleistocene recolonization provided a mechanism for the natural selection of latitudinal adaptive gradients in the mangroves (McMillan 1975, Markley *et al.* 1982). To determine if genetic differentiation could be detected through isozyme analyses, black mangrove populations that had been grown in the laboratory from diverse sources in the Gulf-Caribbean and Pacific Panama and that had shown differentiation in chilling tolerances were examined.

Isozymes have shown the potential for genetic insight in many land plants but little infraspecific variation has been identified in most seagrasses by isozyme studies (McMillan 1980, 1981, 1982; Gagnon, Vadas, Burdick and May 1980; McMillan and Phillips 1981; McMillan and Williams 1980; McMillan, Williams, Escobar and Zapata 1981). In the seagrasses that had shown differences in chilling tolerances (McMillan 1979), there was no corresponding difference in isozyme patterns (McMillan 1980). The uniformity of isozymes within a seagrass species contrasts with the results, for example, of a study in *Spartina* in which Silander (1979) reported isozyme differentiation among individual clones of a single population of *S. patens* (Ait.) Muhl. Similarly, in a Texas population of *S. alterniflora* Lois. adjacent to a black mangrove population, McMillan (unpublished data 1979–1980) also demonstrated characteristic isozyme patterns for individual clones. Although the tool remains generally useful for species separations among the seagrasses, it has yet to be proven of value in identifying infraspecific variation in Gulf-Caribbean seagrasses. While preliminary results (McMillan unpublished data 1979–1984) indicate that isozymes can also be used for species separations in the mangroves, the present investigation tests their usefulness in identifying infraspecific variation in black mangrove.

Although the genus *Avicennia* is taxonomically unsettled, it has received considerable attention, particularly by H.N. Moldenke in a series of papers extending from 1960 through 1977. While the plants of the Gulf of Mexico have generally been referred to typical *A. germinans*, those from the Caribbean and the Pacific coast of the Americas have received diverse treatments. The plants on the Pacific coast as treated by Moldenke are referred to *A. bicolor* Standl., *A. germinans* var. *guayacilensis* (H.B.K.) Moldenke and *A. tonduzii* Moldenke (the latter, Moldenke in personal communication, 1983, feels may be an extreme form of *A. germinans* var. *guayacilensis*). The western Caribbean plants would be treated primarily in *A. germinans* var. *guayacilensis* but would possibly include the other two varieties, var. *cumanensis* (H.B.K.) Moldenke and var. *venezuelensis* Moldenke. The eastern Caribbean plants would include primarily *A. germinans* var. *guayacilensis* and in islands south of St. Croix and Jamaica, *A. schaueriana* Stapf. & Leechman. Most of the plants included in the present study would be referred to *A. germinans.*

MATERIALS AND METHODS

The black mangrove collections from diverse sites in the Gulf of Mexico-Caribbean that were examined for isozyme patterns were those that had been studied previously for chilling tolerances by Markley *et al.* (1982). Propagules had been collected primarily in 1975–1976 and grown subsequently under controlled conditions prior to the isozyme studies. Most of the isozyme investigations were conducted in 1979–1981 on plants that were 3–6 years from rooting. The population from Pacific Panama was not included in the Markley *et al.* (1982) study but showed intolerance of chilling temperatures (2–3° C) when compared with other *Avicennia* populations in 1982 (McMillan unpublished data).

For the isozyme study, leaves were removed from the plants under experimental culture and prepared as outlined for seagrasses (McMillan 1982). The leaves were cut into small pieces and ground on a glass slide with a phosphate buffer, pH 7.0 (with mercaptoethanol and polyvinylpyrrolidone). Filter paper wicks (Whatman No. 3) were dipped into the leaf extracts, blotted to remove excess liquid and inserted into a freshly prepared starch gel for standard electrophoresis. Gels were prepared with Electrostarch lot 392 (O. Hiller, Madison WI), using Tris-glycine and Tris EDTA buffers. After electrophoresis for 3 h at 4° C with an applied voltage of 30 V cm^{-1}, the gels were sliced horizontally and the isozymes visualized following the staining procedures of Brewbaker, Upadhya, Makinen and MacDonald (1968) and Selander, Smith, Yang, Johnson and Gentry (1971).

Although several enzyme systems were explored, phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI) were primarily investigated. For studying the Pacific Panama population, in addition to the above two systems, the following were also studied: alcohol dehydrogenase (ADH), glucose-6-phosphate dehydrogenase (G-6-PD) and aspartate aminotransferase (AAT).

For most populations, nine plants were tested for isozyme patterns. For certain populations, including those from Belize and Panama, 5–24 additional plants were used because of the greater variation in isozyme patterning.

RESULTS

Differences were detected in the isozyme patterns for the black mangroves from the Gulf of Mexico-Caribbean (Figs. 1, 2; Table 1). Plants from diverse latitudes in Mexico (Anton Lizardo, Tuxpan, Ver.; La Pesca, Tamps.) had the predominant patterns for phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI) that were indicated for plants from Harbor Island on the central Texas coast. These plants from the western side of the Gulf of Mexico differed in their predominant patterns of PGM and PGI from plants on the eastern side of the Gulf of Mexico-Caribbean (Biscayne Bay and Key Largo, FL; St. Croix, U.S. Virgin Islands and Port Royal, Jamaica).

The isozyme patterns for plants from the western Caribbean (Belize; San Blas Islands, Panama) and Pacific Panama did not show the uniformity that was indicated for populations on either the western side of the Gulf of Mexico or for those on the eastern side of the Gulf-Caribbean (Figs. 1, 2; Table 1). For both the Belize and the San Blas Islands populations, the pattern for PGI was similar to that of the eastern populations, but the PGM patterns were diverse and included plants with patterns more like the predominant western type as well as those more like the predominant eastern type. The plants from the Pacific Panama population at Punta Chame differed from those of the Caribbean.

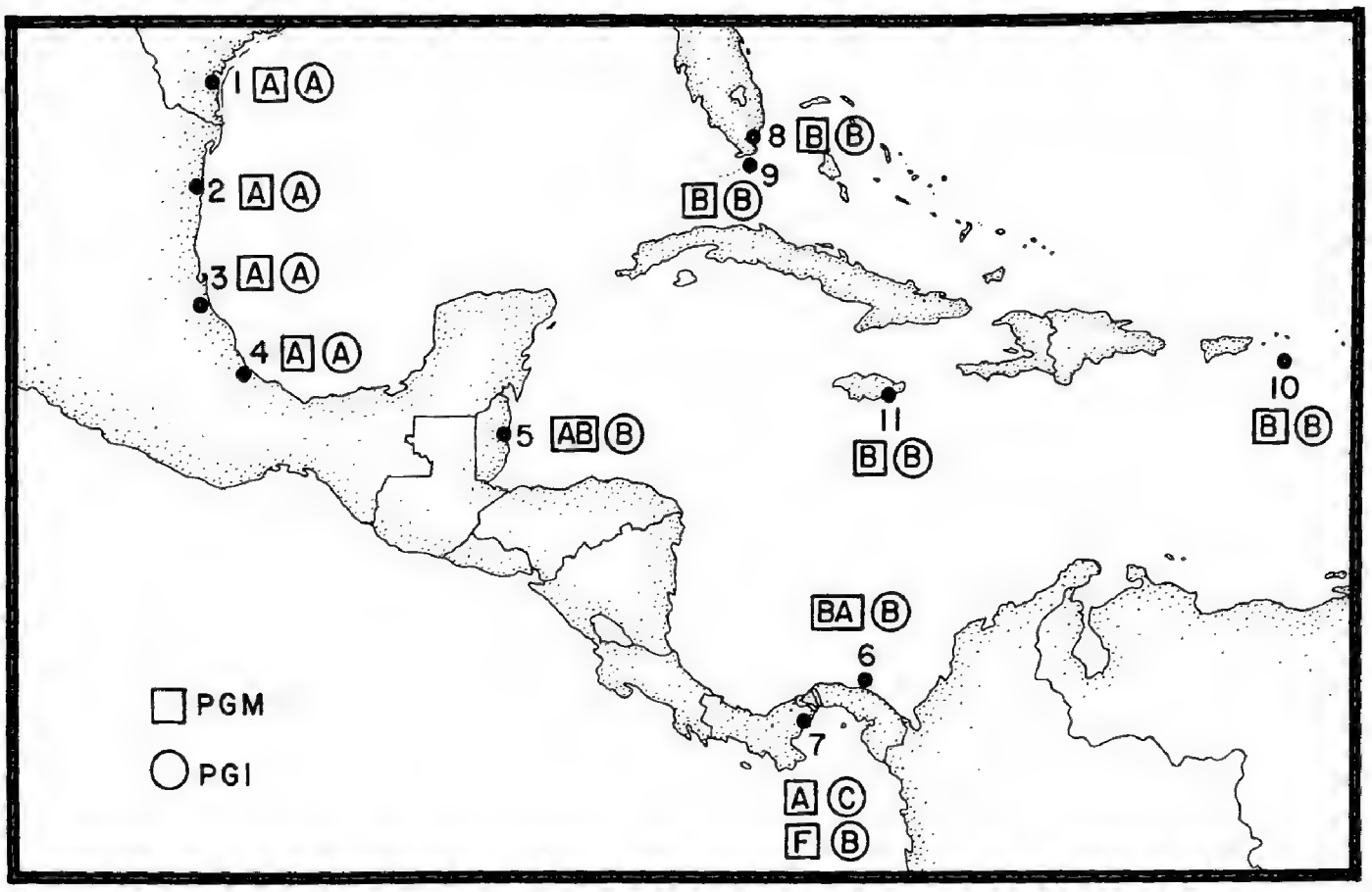

FIG. 1. Map of the Gulf of Mexico-Caribbean and Pacific Panama showing collection sites and predominant patterns for phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI) for laboratory-germinated plants of *Avicennia*. The numbered sites are:

1. Harbor Island, Nueces Co., Texas; 2. La Pesca, Tamaulipas, Mexico; 3. Tuxpan, Veracruz, Mexico; 4. Anton Lizardo, Ver., Mexico; 5. Belize City, Belize; 6. Mosquito Island, San Blas Islands, Panama; 7. Punta Chame, Panama; 8. Biscayne Bay, Dade Co., Florida; 9. Key Largo, Florida Keys, Florida; 10. St. Croix, U.S. Virgin Islands; 11. Port Royal, Jamaica.

See Table 1 for percentages of plants in each population with various patterns of PGM and PGI.

The plants grown from seed collected at Punta Chame on the Pacific coast west of Panama City had isozyme differentiation (Tables 1, 2) that correlated with leaf differences. For six plants, the broadly elliptical leaves had dense whitish pubescence on the lower blade surface (along with heavy salt accumulation) and the isozyme patterns for ADH, AAT and G-6-PD were different from those of 12 plants with elongate-oblong leaves and less pubescence (and less salt accumulation). The six plants with the broadly elliptical leaves showed the PGI pattern indicated for plants on the eastern side of the Gulf Caribbean, but the 12 plants with elongate-oblong leaves differed in PGI patterning from all of the Gulf-Caribbean plants. The six plants with broadly elliptical leaves were referred to *A. bicolor* and the other 12 plants to *A. germinans* var. *guayacilensis* (specimens of each kind that were examined by H.N. Moldenke were verified, tentatively, personal communication, 1983).

DISCUSSION

The isozyme comparisons in *Avicennia* from the Gulf of Mexico-Caribbean and Pacific Panama did not show patterns that correlated with the latitudinal

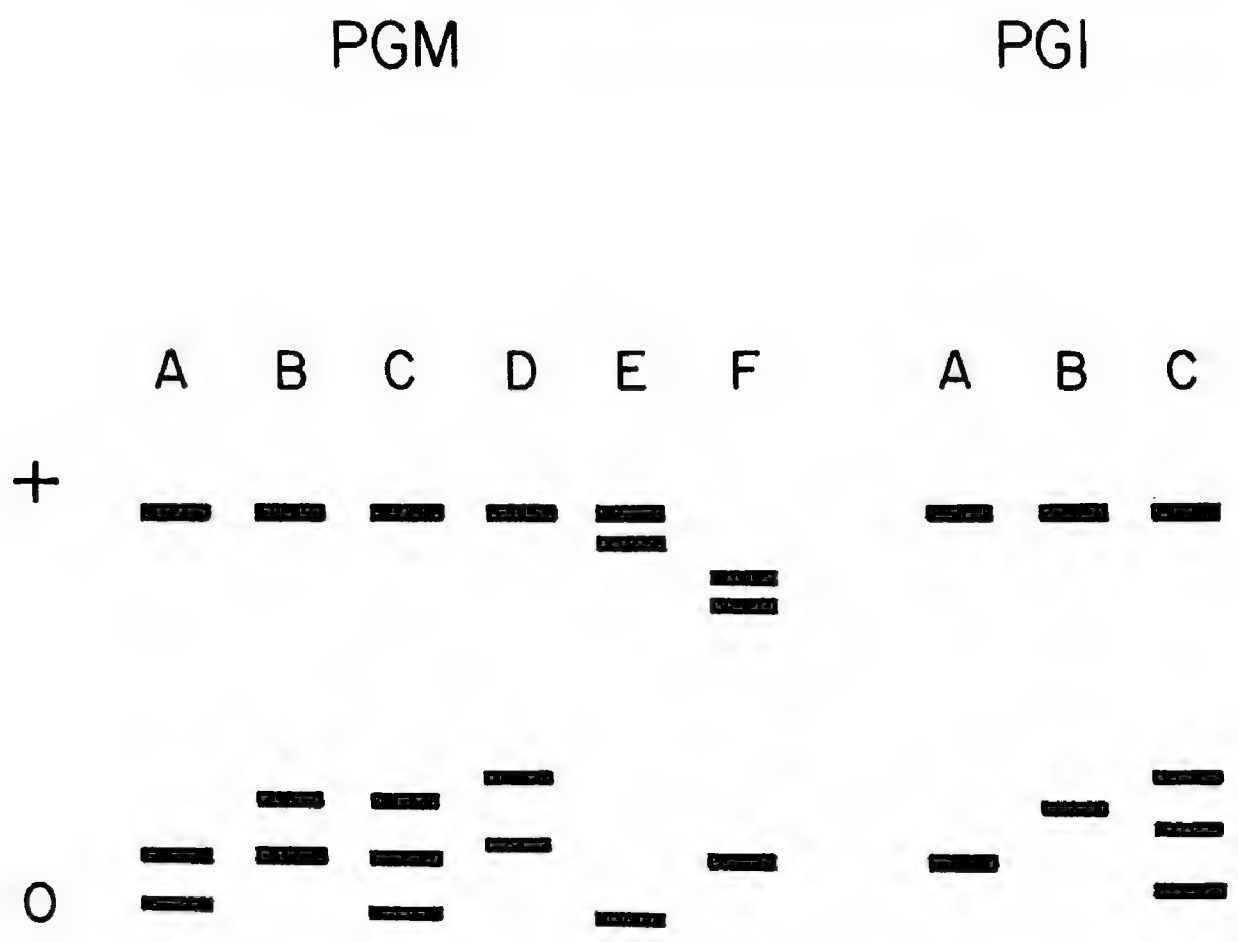

FIG. 2. Electrophoretic banding patterns for two enzyme systems: phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI). The origin of the gel electrophoresis is indicated by (O) and the direction of the anode is indicated by (+). Bands are illustrated according to their relative mobilities within each system but not between systems.

gradients of chilling tolerance reported by McMillan (1975, unpublished data 1982) and Markley *et al.* (1982). Plants from the western side of the Gulf of Mexico showed the same basic pattern for PGM and PGI among the chilling-intolerant plants of southern Mexico as well as among the more chilling-tolerant plants of Texas. Plants from Florida that were more chilling tolerant than those from St. Croix and Jamaica showed the same basic patterns for PGM and PGI as the eastern Caribbean plants. Latitudinal differences that were also associated with chilling tolerance differences among the seagrasses of the Gulf-Caribbean (McMillan 1979) did not show isozyme patterns that correlated with chilling sensitivity (McMillan 1980), as indicated above.

Although the same patterns for PGM and PGI were shown among populations from diverse latitudes on either side of the Gulf-Caribbean, different patterns were characteristic of the two sides. The patterns shown by plants of Mexico and Texas were different from those shown by plants of Florida, St. Croix and Jamaica. Plants from the western Caribbean (Belize and Panama), however, did not show the patterns for either PGM or PGI that were typical of plants of the Western Gulf of Mexico, but plants from both Belize City and Mosquito Island in the San Blas islands of Panama showed a mixture of patterns for PGM.

The difference in isozyme patterns between plants of the western side of the Gulf of Mexico and those of the eastern Gulf-Caribbean led Sherrod and

TABLE 1

Comparison of isozyme patterns for phosphoglucose mutase (PGM) and phosphoglucose isomerase (PGI) in *Avicennia* populations from the Gulf of Mexico-Caribbean and Pacific Panama.

Collection Site[a]	Percentage of plants with patterns[b] of PGM						PGI		
Western sites	A	B	C	D	E	F	A	B	C
1. Harbor Island, Texas	100						100		
2. La Pesca, Tamps., Mexico	89	11					100		
3. Tuxpan, Ver., Mexico	78		22				100		
4. Anton Lizardo, Ver., Mexico	100						100		
5. Belize City, Belize	45	9	18	21	6			100	
6. San Blas Islands, Panama	23	54	15	8				100	
Pacific site									
7. Punte Chame, Panama[c]	37		10	21		33		33	67
Eastern sites									
8. Biscayne Bay, Florida, USA	89			11			100		
9. Key Largo, Florida, USA	78			22			100		
10. St. Croix, US Virgin Islands	100						100		
11. Port Royal,	100						100		

[a] The numbers for the collection sites correspond with those on the map in Fig. 1 Nine plants were compared isozymally for most populations, but 33 plants were studied for Belize, 14 for the San Blas Islands and 18 for Punte Chame.

[b] See Fig. 2 for the patterns of PGM and PGI.

[c] The Pacific Panama plants with pattern F for PGM (33%) and pattern B for PGI had the morphological characteristics of *A. bicolor*. These plants of *A. bicolor* also had patterns for alcohol dehydrogenase, glucose-6-phosphate dehydrogenase and aspartate aminotransferase that were distinct from those of the Pacific Panama plants with morphological characteristics of *A. germinans*. See Table 2.

TABLE 2

Isozyme patterns within an *Avicennia* population from Pacific Panama

Species	Percentage of plants with isozyme patterns[a] for ADH		AAT		G-6-PD	
	A	B	A	B	A	B
A. bicolor[b]	100		100		100	
A. germinans[c]		100		100		100

[a] For each of the three enzyme systems, two isozyme bands were shown. The lower band was faster moving for pattern A than for pattern B for ADH, but the lower band was the slower moving for pattern A for AAT and G-6-PD.

[b] Six of the 18 plants had dense whitish pubescence on the lower leaf surfaces of the broadly elliptical blades. A specimen of one of the six plants was identified tentatively as *A. bicolor* by H.N. Moldenke (personal communication 1983).

[c] Twelve of the 18 plants had less pubescence on the lower surfaces of the elongate-oblong blades. A specimen of one of the 12 plants was identified tentatively as *A. germinans* var. *guayacilensis* by H.N. Moldenke (personal communication 1983). A specimen from the Caribbean population in the San Blas Islands was also identified by H.N. Moldenke as var. *guayacilensis*.

McMillan (1985) to suggest that the recolonization of the northern Gulf by *Avicennia* following its Pleistocene extirpation resulted in genetic isolation and bilateral evolutional divergence. Populations from the western Caribbean that show a mixture of isozyme patterns possibly are the result of mixing oceanic currents that have facilitated genetic communication in that region. As mangrove vegetation recolonized the Gulf of Mexico from sources in the Caribbean, separate prevailing northward currents along the eastern and western Gulf would have maintained the segregation of eastern and western populations.

Among the populations that were included in the isozymal evaluations, most would be included within the typical variety and var. *guayacilensis* of *A. germinans*, and only some of the plants from Pacific Panama would be referred to a different species, *A. bicolor*. The differences among the various enzyme systems that were detected between *A. germinans* and *A. bicolor* indicate that isozyme patterns may be of use in species separations in the mangroves as they have been, as indicated above, in the seagrasses (McMillan 1982).

ACKNOWLEDGMENTS

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LITERATURE CITED

BREWBAKER, J.L., M.E. UPADHYA, Y. MAKINEN and T. MacDONALD. 1968. Isoenzyme polymorphism in flowering plants. III. Gel-electrophoretic methods and application. *Physiologica Plantarum.* 21:930–940.

DAVIS, J.H. 1940. The ecology and geological role of mangroves in Florida. Carnegie Institute of Washington Publication 517, *Papers of the Tortugas Laboratory.* 32:303–412.

GAGNON, P.S., R.L. VADAS, D.B. BURDICK and B. MAY. 1980. Genetic identity of annual and perennial forms of *Zostera marina* L. *Aquatic Botany.* 8:157–162.

LOT-HELGUERAS, A., C. VASQUEZ-YANES and F. MENENDEZ. 1975. Physiognomic and floristic changes near the northern limit of mangroves in the Gulf coast of Mexico. pp. 52–61. In G.E. Walsh, S.C. Snedaker and H.J. Teas (eds.) *Proceedings of the International Symposium on Biology and Management of Mangroves.* Vol. 1. University of Florida, Gainesville.

LUGO, A.E. and C.P. ZUCCA. 1977. The impact of low temperature stress on mangrove structure and growth. *Tropical Ecology.* 18:149–161.

MARKLEY, J.L., C. McMILLAN, and G.A. THOMPSON, JR. 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle* from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany.* 60:2704–2715.

McMILLAN, C. 1975. Adaptive differentiation to chilling in mangrove populations. pp. 62–68. In G.E. Walsh, S.C. Snedaker and H.J. Teas (eds.) *Proceedings of the International Symposium on Biology and Management of Mangroves.* Vol. 1. University of Florida, Gainesville.

———. 1979. Differentiation in response to chilling temperatures among populations of three marine spermatophytes, *Thalassia testudinum, Syringodium filiforme* and *Halodule wrightii. American Journal of Botany.* 66:810–819.

———. 1980. Isozymes of tropical seagrasses from the Indo-Pacific and the Gulf of Mexico-Caribbean. *Aquatic Botany.* 8:163–172.

———. 1981. Morphological variation and isozymes under laboratory conditions in *Cymodocea serrulata. Aquatic Botany.* 10:365–370.

———. 1982. Isozymes in seagrasses. *Aquatic Botany.* 14:231–243.

——— and R.C. PHILLIPS. 1981. Morphological variation and isozymes of North American *Phyllospadix. Canadian Journal of Botany.* 59:1494–1500.

——— AND S.C. WILLIAMS. 1980. Systematic implications of isozymes in *Halophila* section *Halophila. Aquatic Botany.* 9:21–31.

———, S.C. WILLIAMS, L. ESCOBAR and O. ZAPATA. 1981. Isozymes, secondary compounds and experimental cultures of Australian seagrasses in *Halophila, Halodule, Zostera, Amphibolis* and *Posidonia. Australian Journal of Botany.* 29:247–260.

MOLDENKE, H.N. 1960. Materials toward a monograph of the genus *Avicennia. Phytologia.* 7:123–168; 179–232; 259–293.

———. 1967–1977. Additional notes on the genus *Avicennia. Phytologia.* 14:301–320; 326–336; 15:71–72; 470–478; 32:343–370; 436–457; 33:238–270; 34:70–94; 167–203; 36:408–412; 439–450.

SELANDER, R.K., M.H. SMITH, S.Y. YANG, W.E. JOHNSON and J.B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus.* I. Variation in the old field mouse (*Peromyscus polionotus). Studies in Genetics.* 6. University of Texas Publication 7103. pp.49–90.

SILANDER, J.A. 1979. Microevolution and clone structure in *Spartina patens*. *Science*. 203:658–660.

SHERROD, C.L. and C. McMILLAN. 1981. Black mangrove, *Avicennia germinans*, in Texas: past and present distribution. *Contributions in Marine Science*. 24:115–131.

_____ and _____. 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science*. 28:127–140.

Contributions in Marine Science. (1986) Vol. 29:27–36.

SURVIVAL OF RED MANGROVE, *RHIZOPHORA MANGLE*, ON THE GULF OF MEXICO COAST OF TEXAS

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ABSTRACT

Although viable propagules of red mangroves, *Rhizophora mangle* L., arrive on Texas beaches, they have not been observed to naturally establish on the Texas coast. Propagules from Florida that were experimentally established on the southern Texas coast at South Padre Island and at the mouth of the Rio Grande in February and April 1983 survived until the record freeze of December 1983. Propagules of unknown origin that had apparently been artificially established on South Padre Island prior to 1983 had achieved heights ranging up to 2.5 m and had successfully reproduced prior to their destruction in the subfreezing conditions in December 1983. The frequency, duration and/or severity of cold winter temperatures is a prime factor governing the distribution and abundance of mangrove species in the northern Gulf of Mexico, including the red mangrove.

INTRODUCTION

Although four mangrove species occur in the northern Gulf region, only black mangrove, *Avicennia germinans* (L.) L., has established populations in Texas, Louisiana and extreme northern Florida. *Rhizophora mangle* L., red mangrove, propagules are washed ashore in a viable condition on Texas beaches but no naturally established plants have been observed from this beach drift (McMillan 1971, Correll and Johnston 1970, Gunn and Dennis 1973). The white mangrove, *Laguncularia racemosa* (L.) Gaertn., and the button mangrove, *Conocarpus erectus* L, occur with the black and red mangrove approximately 300 km south of the Texas border in northeastern Mexico at LaPesca, Tamaulipas (23° 47′ N lat.) (Lot-Helgueras, Vasquez-Yanes and Menendez 1975; McMillan unpublished data 1975–76) and on the Florida Gulf Coast to near 29° N lat. at Cedar Key (Davis 1940, Lugo and Zucca

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1977). The more northern extension of black mangrove populations is a result of greater chilling tolerance (Markley, McMillan and Thompson 1982; McMillan and Sherrod 1986) as a consequence of the natural selection of latitudinal adaptive gradients on both sides of the Gulf of Mexico.

Since the red mangrove extends up both coasts of Florida to approximately the same latitude as Galveston, Texas, this study was aimed at determining if development of latitudinal adaptive gradients for that species had progressed further on the east side of the Gulf than on the west. Experiments were undertaken in the field and laboratory to determine if plants from northern Florida could survive winter conditions in Texas.

To determine the survival potential of red mangroves in the extreme northern Gulf of Mexico, propagules were experimentally established on the southern Texas coast. Propagules from northern Florida were studied in plantings north of the town of South Padre Island and at the mouth of the Rio Grande, near the southern-most tip of Texas. Additionally, previously established plants, within a black mangrove population between the causeways on South Padre Island, and of unknown origin were also monitored. The effects of subfreezing conditions of December 1983 on the red and black mangroves were studied and compared.

FIG. 1. Transplanted red mangroves along the shallow margin of Laguna Madre, *ca.* 6 km north of the Queen Isabella Causeway, on South Padre Island. This photograph in February 1983 shows the dense stand of *Spartina alterniflora* that later expanded into the mangrove planting area during the summer of 1983. Scattered bushes (under 1 m in height) of black mangrove, *Avicennia germinans*, occurred in the vicinity, but are not shown in photograph.

MATERIALS AND METHODS

Rootless propagules of red mangroves that were received from their northern-most distribution point at Daytona Beach, Florida (29° 15′ N lat.) in October 1982 were rooted under controlled conditions prior to being transplanted on the coast of southern Texas and studied in the laboratory. In February 1983, 75 seedlings were planted on the Laguna Madre shoreline of South Padre Island near the northern end of the City of South Padre Island in an area adjacent to a *Spartina alterniflora* Lois. population with scattered black mangroves (Fig.1). The substrate was fine sand near the mean high water line. A second planting of 80–90 seedlings was made in April 1983 in a muddy substrate adjacent to the mouth of the Rio Grande and at the site of the tallest black mangroves in Texas (Sherrod, unpublished data 1982) (Fig. 2). Rooted plants from this Daytona Beach site as well as from a southern population near Miami were tested for temperature intolerances in the laboratory along with plants of Caribbean origin from Union Island, St. Vincent and the Grenadines.

Established plants of unknown origin were discovered within a black mangrove population on South Padre Island. Due to their relatively uniform size, density, and spacial arrangement, these plants appeared to have been artificially established, perhaps several years prior to the 1983 discovery. In 1983, these plants were observed to be flowering and producing viable propagules, some of which had successfully established prior to December 1983. These red mangroves of unknown origin were measured and monitored during 1983 and in 1984–1985 following the December freeze.

FREEZING CONDITIONS OF DECEMBER 1983

The Texas coast experienced one of the most severe, extended periods of low winter temperatures in recent history. Subfreezing temperatures pre-

FIG. 2. Transplant site for red mangroves along the mouth of the Rio Grande. This photograph in April 1983 also shows some of the tallest black mangroves (to near 6 m in height) in Texas.

vailed during a 9-day period in late December 1983 with extremes plummeting to the −6 to −10° C range on several occasions during that period (NOAA 1983). Temperatures to −6.11° C were recorded at Brownsville, *ca.* 25 km southwest of South Padre Island, and 54 consecutive hours below 0° C were recorded on 24–26 December (Table 1).

Although air temperatures were not recorded in the immediate vicinity of the red mangroves on South Padre Island, some temperatures were taken at Port Isabel, on the opposite side of the Laguna Madre. Minimum tempera-

TABLE 1

Number of Hours at Temperatures below 0°C at Brownsville, Texas on 24–26 December 1983[1]

Number of Hours	Temperatures (°C)
7	0 to -1.67
12	-1.67
11	-1.67 to -3.89
10	-3.89
8	-3.89 to -5.56
1	-5.56
2	-5.56 to -6.11
3	-6.11

[1] Temperatures were recorded below 0°C for 54 consecutive hr between 4:46 a.m. on 24 December and 10:45 a.m. on 26 December. On 24 December, the temperature lowered to -3.89°C between 10:49 and 11:53 a.m. and remained at this temperature for 10 hr. On 25 December, the lowest temperature, -6.11°C was recorded at 4:47 a.m. and remained at this point for 3 hr. The temperature rose to -1.67°C at 1:45 p.m. on 25 December and remained near this temperature until 10:45 a.m. on 26 December. A previous low temperature of -2.78°C was recorded in 1963. The NOAA temperature were recorded at a point approximately 25 km southwest of South Padre island and *ca.* 20 km west of the mouth of the Rio Grande.

tures were recorded to −6.66° C on 23 December and to −6.11° C on 24–25–26 December (only one minimum recorded during the three day period) at the Port Isabel Water Plant. Minimum temperatures of −3.33° and −2.78° C were recorded on 27 and 29 December.

Notes taken by the Texas Parks and Wildlife Department (unpublished data 1984) indicate that water temperatures in Laguna Madre were near 0° C during the extended freeze. On 25 December, water temperatures in the shallow seagrass beds adjacent to South Padre Island ranged from 2.0 to 0.0° C in the period from 11 AM to 1 PM. Ice was observed at 1 PM in shallow water from South Padre Island into the Laguna Madre for *ca.* 0.4 to 0.8 km, adjacent to the area with red mangroves of unknown origin.

RESULTS

A total of 53 red mangrove plants of unknown origin was discovered on the Laguna Madre coast of South Padre Island within a black mangrove population that extends between the new Queen Isabella Causeway and the state fishing pier (old causeway). The plants were first observed in 1983 but had established at this site prior to 1983. The 50 larger plants were mostly confined to two tidal inlets and were in a spaced arrangement indicating the possibility that several clusters of propagules had been planted in the muddy substrate. There were 6 clusters of 5 plants, 1 with 4 plants, 3 with 3 plants, 1 with 2 plants, and 5 isolated individual plants. If each cluster represented an original planting of 5 propagules, a total of *ca.* 75 propagules might have been introduced at this site, but if the surviving groups with fewer than 3 plants were "escapees" from the clusters of 5 propagules, then a total of *ca.* 50 might have been in the original introduction. Two small stature individuals and one recently established seedling probably represented progeny of the original plantings. Many of the red mangroves were flowering in 1983 and some propagules were projecting from the fruits attached to the plants.

In 1983, the red mangroves were well established when first inspected in March. (Fig. 3). For seven of the tallest plants that were tagged and measured, the heights ranged from 1.5 to 2.5 m. When all of the plants were reinspected and measured in August 1985 following their demise from the freeze (Fig. 4), 19 still had desiccated apical buds on the main stems and ranged in height from 1.05 to 2.25 m (mean 1.68 m). Although the main stems had been broken on several plants, all of the plants had standing stems over 0.5 m, only 4 were less than 1.0 m, and 17 were 2.0–2.45 m in height. The seven plants measured in March 1983 had stem diameters ranging from 0.55 to 1.58 cm. The same stems measured in 1985 ranged in diameter from 1.0 to 1.8 cm indicating that the plants had achieved growth between March and December 1983, prior to the freeze.

When each plant was rechecked to determine survival in February and August 1984, following the freeze, none had any green tissue. In August, *ca.* 40% of the black mangroves in the immediate vicinity of the red mangroves had resprouted from the basal 0.3 m. In June 1985, each plant was again

FIG. 3. Students at the Coastal Studies Laboratory tagging and measuring red mangroves on South Padre Island in March 1983. This population of 53 red mangroves was discovered in 1983 and ranged in height up to 2.5 m.

checked, but at that time, no evidence of survival was seen in the red mangroves. Most of the black mangroves that had resprouted were flowering.

Of the 75 rooted red mangroves from northern Florida that were transplanted to South Padre Island in February 1983 (Fig.1), 50 surviving plants were accounted for in August. Most had some stem growth and new leaf production. The *Spartina* stand had grown out beyond the red mangroves and completely engulfed them. None of the red mangroves showed any leaf regeneration in 1984 after the freeze and were killed by the subfreezing conditions.

Among the 80–90 rooted red mangroves from northern Florida that were transplanted to the mouth of the Rio Grande in April 1983, approximately 60 survived through the summer. Seven plants measured for stem elongation in June 1983 showed growth of 9–22 cm with a mean growth of 15.2 cm. As with those transplanted to South Padre Island, all were killed by the subfreezing conditions in December.

Red mangroves from northern Florida were also tested in the laboratory during 1983 for an assessment of chilling tolerances. In a comparison of 20 plants from northern Florida near Daytona Beach and 20 from southern Florida near Miami that were grown from propagules collected in the fall of 1982, the plants from both sites showed slight dysfunction (wilting of some

FIG. 4. Red mangroves on South Padre Island that were killed by the sub-freezing temperatures of December 1983. This photograph in August 1985 shows the nearly intact skeletons of red mangroves in a cluster at the fringe of the black mangrove population which resprouted after the December freeze. The apical buds were still intact on many of the branches of the red mangroves.

leaves and stem tips) but no permanent chilling injury from exposure to chilling temperatures of 4° C for 5 days. Ten older plants (8–9 yr from rooting, from cultures used by Markley *et al.* 1982) of southern Florida (Miami) origin and 10 from northeastern Mexico (La Pesca, Tamaulipas) showed little dysfunction after exposure to similar chilling conditions, but those of comparable age from St. Croix, U.S. Virgin Islands, showed extensive chilling injury and 4 of the 10 plants subsequently died. The red mangroves from northern and southern Florida continued to survive in the laboratory through 1983 and were tested further in 1984.

Plants that were *ca.* 18 months from rooting were chilled to 2–3° C for 24 hours. Plants from both northern and southern Florida survived the chilling conditions, but 60% of the southern plants (Miami) showed some physiological dysfunction and injury while only 12% of the northern plants (Daytona

Beach) showed these injury symptoms. Plants from the more tropical site in the Caribbean (St. Vincent) were all damaged by the 24-hour chilling treatment.

In another test, the plants from northern Florida were compared with those from St. Vincent. Plants that had been grown at temperatures of 30°/24° C (day/night) were moved into a growth chamber with a constant temperature of 16° C for 5 days. Each of 5 plants from Florida showed no dysfunction under these conditions and only 1 of the 5 from St. Vincent had wilted leaves. Subsequently, after an additional five days at 13° C, all 10 plants showed some physiological dysfunction with wilting of leaves and stem tips. The physiological dysfunction continued during a subsequent 5 additional days at 10° C, but permanent injury was shown only by the St. Vincent seedlings. When the plants were returned to 30°/24° C after 15 days of chilling conditions, 4 of the 5 St. Vincent plants died, but all of the Florida plants survived.

DISCUSSION

Propagules of red mangrove that frequently arrive on Texas beaches from February through May have not been reported to naturally establish, but these propagules have been established successfully in experimental cultures. Propagules collected on Gulf beaches along Mustang Island (Port Aransas) were used in studies of chilling tolerance by Markley *et al.* (1982). Laboratory-cultured plants were transported back to Port Aransas where they survived over winter in 1975–1976 in an experimental pond. Viable propagules were collected on the Gulf beaches of South Padre Island in both 1984 and 1985 (McMillan unpublished data), but all of the collection sites on sandy beaches were unlikely for successful establishment. Although it is possible that propagules could move through the passes along the Texas coast into various bays, including Laguna Madre, they have not been observed to do so or to establish naturally in those sites (McMillan unpublished data) where muddy sediments are favorable for their establishment.

Although the origin is not certain for the 50 large red mangroves that were discovered in 1983 on the Laguna Madre shore of South Padre Island, their spaced arrangement in plant clusters indicates that they were not distributed at random from floating debris. It seems most likely that the plants were established by the insertion of clusters of propagules into the muddy sediments at 10–15 points within a black mangrove population. Although the age of the plants is not known, they were vigorously growing and flowering during the summer of 1983 and had survived the winter of 1982–83 (and possibly several previous winters). The presence of a few small plants in 1983 indicated some natural propagation may have occurred in this red mangrove population.

The two experimental plantings of red mangrove seedlings of northern Florida origin indicate a rapid establishment potential of this species in Texas. The plantings on South Padre Island and at the mouth of the Rio Grande had grown during their first year of establishment.

The extended period of subfreezing conditions in December 1983 led to the total destruction of the red mangroves in Texas. The discovered population with 50 plants that ranged in height to near 2.5 m as well as the smaller plants that may have resulted from natural propagation from these older, flowering plants did not survive the freeze. Neither of the experimental plantings of 1983 showed any subsequent survival following the extended freeze.

Although the effects of subfreezing temperatures were not explored in the laboratory, the consequences of chilling temperatures (above freezing) were studied. The northern Florida seedlings that were experimentally planted in southern Texas in 1983 showed a greater ability to withstand chilling conditions (4–16° C) than was shown by plants of more tropical origin in the Caribbean. Markley *et al.* (1982) reported that all of the red mangroves that were transplanted to an experimental outdoor pond at Port Aransas on the Texas coast showed injury from 1975–1976 winter conditions, but that the plants of most tropical origin, Panama and Jamaica, failed to survive. In the above study at Port Aransas, plants grown from beach debris collected on the Texas coast (possibly of northeastern Mexico origin) and plants grown from propagules collected in southern Florida (Miami) survived a winter with 24 h below 4° C in December 1975 and 96 h below 4° C in January 1976. While plants of Florida origin as well as those from northeastern Mexico might be able to withstand the average winter conditions on the Texas coast with light freezes, the extreme subfreezing conditions of December 1983 exceeded the low temperature tolerances of red mangroves.

The effect of the 1983 freeze on red mangroves in Texas was more disastrous than that reported for the January 1977 freeze in Florida by Lugo and Zucca (1977). Although temperatures to −2.7° C and at or below 0° C for 5 days were recorded for Cedar key (29° 08′ N lat.) adjacent to Seahorse Key (unofficially to −5.5° C) and the location of the northern-most populations of red mangrove on the Gulf coast of Florida, Lugo and Zucca (1977) reported that some red mangroves retained green leaves after the freeze and that those plants were still growing in September. None of the red mangroves transplanted to southern Texas from northern Florida or of unknown origin discovered on South Padre Island survived the 1983 freeze.

These studies along with those of Markley *et al.* (1982) clearly indicate that latitudinal adaptive differentiation occurs in red mangrove populations of the northern Gulf of Mexico and that red mangroves of northern Florida appear to have progressed further toward genetic adaptation to chilling temperatures. The plants of northern Florida are occasionally exposed to mild freezing conditions and have been shown to survive and reproduce. Plants of unknown origin which were established on the southern Texas coast also survived one or more normal winters with recordings of chilling conditions and mild freezes but were killed by the record freeze of 1983. While the northern-most locations of red mangroves in Florida correspond in latitude with Galveston on the northern Texas coast, indefinite survival of these plants is precluded on the extreme northern Gulf of Mexico coast by the frequency, duration and severity of freezing temperatures. Northern Florida is provided with a slight

buffer from the effects of northern cold fronts by the usually east by southeasterly direction these fronts approach Florida over the Gulf moderating the cold temperatures. These fronts approach the Texas coast from an inland direction with little moderation of temperatures.

The physiological-biochemical mechanisms for chill or freeze tolerance in *Rhizophora* were not investigated, but Markley *et al.* (1982) correlated cellular membrane structure and fatty acid composition with chill tolerance in *Avicennia* that was related to genetic inheritance. It is likely that similarly inherited properties in *Rhizophora* have resulted in latitudinal differentiation in response to chill tolerance in the Gulf of Mexico and Caribbean. However, the inability to resprout in *Rhizophora* following significant foliar and apical stem damage from severe freezes may preclude the red mangrove from the more northerly extremes as *Avicennia*, which readily resprouts from lateral branches or from the main trunk.

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LITERATURE CITED

CORRELL, D.S. and M.C. JOHNSTON. 1970. *Manual of the Vascular Plants of Texas.* Texas Research Foundation, Renner, Texas. 1881 p.

DAVIS, J.H. 1940. The ecology and geological role of mangroves in Florida. Carnegie Institute of Washington. Publication 517. *Papers of the Tortugas Laboratory.* **52**:303–412.

GUNN, C.R. and J.V. DENNIS. 1973. Tropical and temperate stranded seeds and fruits from the Gulf of Mexico. *Contributions in Marine Science.* **17**:111–121.

LOT-HELGUERAS, A., G. VASQUEZ-YANES and F. MENENDEZ. 1975. Physiognomic and floristic changes near the northern limit of mangroves in the Gulf coast of Mexico. pp. 52–61. In G.E. Walsh, S.C. Snedaker and H.J. Teas (eds.) *Proceedings of the International Symposium on Biology and Management of Mangroves.* Vol. 1. University of Florida, Gainesville.

LUGO, A.E. and C.P. ZUCCA. 1977. The impact of low temperature stress on mangrove structure and growth. *Tropical Ecology.* **18**:149–161.

MARKLEY, J.L., C. McMILLAN and G.A. THOMPSON, JR. 1982. Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle*, from the western tropical Atlantic and Pacific Panama. *Canadian Journal of Botany.* **60**:2704–2715.

McMILLAN, C. 1971. Environmental factors affecting seedling establishment of the black mangroves on the central Texas coast. *Ecology.* **52**:927–930.

_____ and C.L. SHERROD. 1986. The chilling tolerance of black mangrove, *Avicennia germinans,* from the Gulf of Mexico coast of Texas, Louisiana and Florida. *Contributions in Marine Science.* **29**:000–000.

NOAA. 1983. Local Climatological Data, Monthly Summary: Galveston, Corpus Christi, and Brownsville, Texas. ISSN 0198-5078, 4977, and 4950.

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CHANGES IN CHLOROPHYLL *A* CONCENTRATIONS IN A SHALLOW WATER COLUMN DURING A SOLAR ECLIPSE

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ABSTRACT

Calcasieu Lake, a broad, shallow estuary in southwest Louisiana, was sampled before, during and after the solar eclipse on 30 May 1984, and again under comparable conditions the next day. Although there was no distinct vertical pattern of chlorophyll *a* among depths in the water column on either day, median concentration of chlorophyll *a* in the water column increased during the eclipse and decreased afterward. The difference in chlorophyll concentration between paired observations on the two days was significantly correlated with the difference in light dynamics between the two days. We propose that changes in chlorophyll *a* concentration in the water column during the eclipse may have resulted from vertical migration of microflagellates from very near the bottom in response to the eclipse.

INTRODUCTION

Solar eclipses have proven to be valuable "natural experiments" in the study of diel vertical migration (Ferrari 1976). Most such studies have concerned the effects of rapidly changing light levels on zooplankton distribution (Sherman and Honey 1970; Bright, Ferrari, Martin and Franceschini 1972). However, other studies have examined changes in bioluminescent activity and the depth of sonic scattering layers (Backus, Clark and Wing 1965) and the behavior of marine organisms, including pelagic fishes, in outdoor enclosures (Skud 1967).

Although some phytoplankters are known to be diel vertical migrators (*e.g.* Eppley, Holm-Hansen and Strickland 1968; Blasco 1978; Lannergren 1979; Oliver and Walsby 1984, Anderson and Stolzenbach 1985), the only study of phytoplankton response to a solar eclipse (Franceschini, Bright, Caruthers, El-Sayed and Vastano 1970) yielded equivocal results. Franceschini *et al.* (1970) found that whereas the concentration of chlorophyll *a* in near-surface waters of the Gulf of Mexico did not appear to vary in response to a solar

eclipse, integrated samples from the surface to 50 m depth indicated a decrease in chlorophyll *a* concentration during and following the eclipse. However, Franceschini *et al.* (1970) did not feel that their data were adequate to separate phytoplankton responses to the eclipse from other possible explanations, such as increased grazing by zooplankton which migrated upward during the eclipse.

We investigated the vertical distribution of phytoplankton biomass during and after a nearly total solar eclipse at the site of an ongoing long-term study. Since we expected that the biomass would be composed largely of phytoflagellates (Maples, Beck, Casserly, Turner and Vecchione 1984), we hypothesized that the depth of the peak biomass would shift during the eclipse.

MATERIALS AND METHODS

Study Area. Calcasieu Lake (30° 00′ N latitude, 93° 20′ W longitude) is the largest of a series of broad, shallow estuarine lakes linking the Calcasieu River in southwest Louisiana with the Gulf of Mexico. Our study area was in Turner's Bay at the north end of Calcasieu Lake. This area was chosen because McNeese State University has been conducting multidisciplinary studies there since February 1981. Aside from a dredged ship channel, water depths average < 2 m and the water column is not usually stratified (Stubblefield, Lascara and Vecchione 1984). The solar eclipse occurred on 30 May 1984. Maximum coverage of the sun in our area (*ca.* 90% was at approximately 1108 CDT.

Field and Laboratory Protocol. Water samples and ancillary measurements described below were collected every 30 min from 0915 to 1245 both on the day of the eclipse and on the following day. In order not to confuse vertical migration with the advection of phytoplankton patches past a fixed station (Sinclair, Chanut and El-Sabh 1980; Levasseur, Therriault and Legendre 1983), we deployed a drogue buoy at the beginning of sampling each day. All samples were collected in the vicinity of this drifting marker and therefore presumably came from a single water mass on each day.

Because the water depth in this area was *ca.* 1.0–1.5 m, we collected water with a hand pump (after allowing sufficient pumping for the water to cycle through the hose and pump) at the surface, at 0.5 m, and at 1.0 m. Two 500 ml samples were collected, one preserved with Lugol's iodine and the other transported to the laboratory at ambient temperature in an insulated cooler. Samples were not replicated because our experience has been that at this time of year, in this part of the estuary, variability in chlorophyll among replicate samples is quite low. Our long-term project includes triplicate samples; in eight sets of triplicate samples which are comparable to those reported here, the average coefficient of variability (CV = standard deviation divided by mean) was 0.13 while the CV range was 0.04–0.23. We therefore decided to increase the number of observations and use non-parametric statistics as described below.

Salinity and temperature were measured for each sample by refractometer and mercury thermometer, respectively. Solar radiation ($\mu E/s/m^2$ photosynthetically active radiation: 400–700 nm waveband) was measured above the surface and at each sampled depth using a LI-COR quantum sensor with integrating quantum radiometer.

In the laboratory, aliquots of 100 ml from the unpreserved samples were vacuum filtered at 25 psi through 47 mm Gelman glass filter. Each filter was wrapped in aluminum foil and frozen until processed. Vacuum pressure of 25 psi was considered to be adequate because we had previously examined filtrates of water from this study area using both fluorometry and microscopy and had found no evidence of cell-rupture or ineffective filtration at this pressure using Gelman glass filters. All samples were processed within 72 h of collection. Methods for pigment extraction, phaeopigment and chlorophyll *a* determinations (fluorometric), and pigment calculations were those described by Strickland and Parsons (1972). The iodine-preserved samples were examined by phase-contrast light microscopy for taxonomic composition.

Statistical Methods. Differences in chlorophyll concentration among depths were tested using the Friedman non-parametric analysis of variance. Since the variance among depths was not significantly different from random, subsequent analyses were based on the median chlorophyll concentration for each sampling period. Paired sampling periods from the two days were compared for median chlorophyll concentration using the Wilcoxon matched-pairs signed-ranks test. Spearman's rank correlation coefficient was calculated for the relationship between solar radiation above the surface and median chlorophyll concentration. Finally, the difference in above-surface radiation between the two days was compared with the difference in median chlorophyll concentration between days using Spearman's rank correlation coefficient.

RESULTS

The track of the drogue buoy was very similar, approximately due south, on both days. Fortunately, weather conditions were also similar (no cloud cover, ENE winds 10–15 mph) on both days. Water temperatures were almost identical (24.5–26.5° C) on the two days, but salinity was somewhat higher ($4–10 \times 10^{-3}$) on the day after the eclipse than on the day of the eclipse ($2–4 \times 10^{-3}$).

Solar radiation above the surface on the day of the eclipse decreased from 1579 $\mu E/s/m^2$ at 0945 CDT to 211 $\mu E/s/m^2$ at 1110 CDT, then increased to 1980 $\mu E/s/m^2$ at 1215 CDT. Before the eclipse, light intensity at 1 m depth was 35 $\mu E/s/m^2$ or about 2.2% of the intensity above the surface. By 1110 CDT, light at 1 m depth had decreased to 2 $\mu E/s/m^2$ (0.9% of above-surface radiation). The light intensity just below the surface at 1110 CDT was 179 $\mu E/s/m^2$, which was similar to that at 1 m depth following the eclipse (107 $\mu E/s/m^2$ at 1215 CDT). On the day after the eclipse, light intensity above the surface increased steadily from 1324 to 2170 $\mu E/s/m^2$ while light at all three depths in the water column fluctuated around increasing trends. Light penetration at 1 m depth ranged from 4.5% to 1.8% of above-surface intensity.

As mentioned above, variability in the concentration of chlorophyll *a* among depths followed no distinct pattern (Fig. 1) and was not significantly different from random on either day (30 May: $\chi^2 = 1.75, p = 0.417$; 31 May: $\chi^2 = 3.00, p = 0.223$). Median chlorophyll *a* concentration on the day of the eclipse increased until maximum solar coverage (1110 CDT) and decreased afterward (Fig. 1). On the day of the eclipse, median chlorophyll concentration was negatively correlated with above-surface light intensity ($\rho = -0.476$) but the relationship could not be considered to be statistically significant ($p = 0.116$). Conversely, on the next day the relationship between median chlorophyll concentration and light intensity was positive and significant ($\rho = 0.647, p = 0.042$). There was a strong negative correlation ($\rho = 0.833, p = 0.005$) between the difference in light intensity and the difference in chlorophyll *a* concentrations at matched times on the two days.

Examination of the preserved samples indicated that most of the organisms in the water column throughout this period were autotrophic microflagellates (Cryptophyceae and Euglenophyceae). Our methods, however, proved inadequate for detailed taxonomy or specific cell-counts for these nannoplankton.

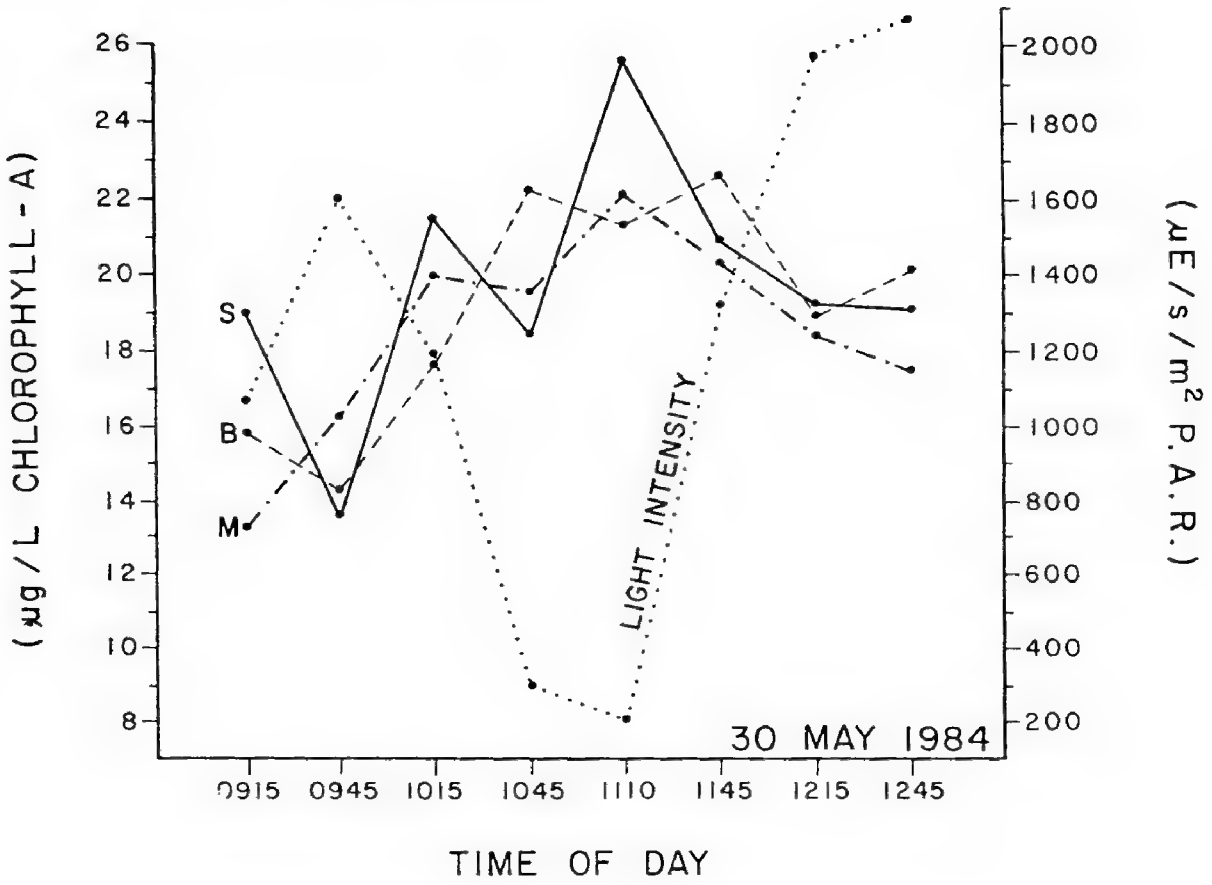

FIG. 1. Temporal changes in chlorophyll *a* concentrations at three depths in the water column and concurrent changes in light intensity above the surface.

S — near surface (0.1 m depth);

M — mid-depth (0.5 m);

B — near-bottom (1.0 m);

P.A.R. — photosynthetically active radiation.

DISCUSSION

The chlorophyll concentrations which we found during this study were similar in magnitude to those resulting from our long-term study. The mean and standard deviation of chlorophyll *a* concentration from four stations in the Turner's Bay area in May 1984 was 18.59 and 8.95 μg/L, respectively. In May 1985, the mean concentration was 18.94 μg/L and the standard deviation was 9.12 μg/L.

The patterns of chlorophyll concentration which we observed during and after the eclipse, though significant, did not match our *a priori* expectations. We expected to detect a decrease in biomass near the bottom (1 m depth) concurrent with an increase in biomass higher in the water column during the eclipse. However, wind mixing may have been sufficient to randomize the vertical distribution of phytoplankton above the bottom.

Temporal changes in the concentration of chlorophyll *a* in the water column may have resulted from one or more potential processes, including vertical migration from the unsampled layer very near the bottom. Alternate explanations include temporal variability in grazing pressure (Therriault and Platt 1978), small-scale spatial variability (Levasseur *et al.* 1983), rapid cell division (Rivkin, Voytek and Seliger 1982) or chlorophyll synthesis (Auclair, Demers, Frechette, Legendre and Trump 1982), and passive resuspension of cells from the sediment-water interface (Roman and Tenore 1978).

Although it is conceivable that grazing pressure from zooplankton decreased during the eclipse, this is an unlikely explanation. A longstanding concept in zooplankton ecology is that decreasing light levels trigger both vertical migration and increased feeding activities (Enright 1977, Pierre 1979, Ringelberg 1980). Such an explanation would also be contrary to the interpretation by Franceschini *et al.* (1970) that decreased chlorophyll concentration in the Gulf of Mexico during an eclipse may have resulted from increased grazing by vertically migrating zooplankton during the eclipse. Furthermore, we noted that numbers of zooplankton in our samples were quite low.

A more likely alternative, and one which we cannot refute, is that of spatial variability. We attempted to minimize this possibility by Lagrangian methods. However, the effectiveness of a drogue buoy is lessened when vertical current shear occurs within the depth range of the drogue. Such shear is quite likely in a shallow system like Calcasieu Lake because of bottom friction, and our drogue covered most of the depth of the water column. Thus the buoy may not have remained in a distinct water mass at all depths as planned. It is therefore possible that we encountered a small patch of phytoplankton concurrent with, but unrelated to, the eclipse. Within this scenario, the lack of similar patch structure on the second day may be related to salinity differences between the two days. If turbulence on both days, though, was sufficient to homogenize the vertical distribution of phytoplankton, the occurrence of a small discrete patch coincident with the eclipse seems to be less parsimonious an explanation than vertical migration.

Rapid cell division and chlorophyll synthesis are known to occur but have not been shown to be important on the time scales (*ca.* 1 h) in which we found

changes in chlorophyll concentration. Rapid physiological changes are probably coupled with environmental periodicity (Auclair *et al.* 1982), so for estuarine phytoplankton a tidal period (*ca.* 6 h) is a likely minimum scale for consistent physiological variability. It is possible, though, that chlorophyll synthesis was suppressed by mid-day light levels (Falkowski 1981) on 31 May but not during the eclipse.

Passive resuspension of cells by turbulence may have occurred, but since wind velocities were constant throughout the two-day study a single brief pulse of resuspension during the eclipse is an unlikely coincidence.

The explanation that we believe to be most likely is that the microflagellates which we found in our samples were concentrated very near the bottom before the eclipse. We were not able to distinguish between cells which would ordinarily be considered epibenthic microflora and those which are nannoplanktonic. However, Stubblefield *et al.* (1984) have shown that some zooplankton species concentrate very near bottom in Turner's Bay. Furthermore, Maples *et al.* (1984) have found that the taxa of phytoplankton in the stomachs of oysters from this area are different from those in the water column, indicating a distinct epibenthic assemblage. We propose that the flagellates from this assemblage migrated upward in response to decreased light levels during the eclipse, making them vulnerable to our sampler. Since light intensity near the surface during maximum solar coverage was similar to that near the bottom before and after the eclipse, it can be argued that the flagellates were attempting to maintain position relative to a preferred isolume (Ringelberg 1980). Anderson and Stolzenbach (1985) have shown that diel vertical migration from a subsurface layer in response to a preferred isolume and avoidance of the surface is an important mechanism for retention of dinoflagellates in a shallow well-mixed estuary. Active downward migration with increasing depth of the isolume would be required to remove the flagellates from the turbulent water column following the eclipse.

The importance of this interpretation is twofold: Microflagellates are often abundant in shallow estuarine and coastal areas (*e.g.*, Ignatiades 1979, Bowman, Esaias and Schnitzer 1981; Furnas 1983; Sellner 1983); and phytoplankton biomass, measured as chlorophyll *a* concentration in the water column, is often a controlling parameter in estimates of ecosystem productivity (*e.g.*, Harris 1980, Cole and Cloern 1984, Peterson and Festa 1984). If abundant vertically migrating microflagellates are concentrating very near the bottom at the time that biomass is measured, estimates of productivity may be seriously biased.

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LITERATURE CITED

ANDERSON, D.M. and K.D. STOLZENBACH. 1985. Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance. *Marine Ecology — Progress Series.* **25**:39–50.

AUCLAIR, J.C., S. DEMERS, M. FRECHETTE, L. LEGENDRE and C.L. TRUMP. 1982. High frequency periodicities of chlorophyll synthesis in estuarine phytoplankton. *Limnology and Oceanography.* **27**:348–352.

BACKUS, R.H., R.C. CLARK and A.S. WING. 1965. Behavior of certain marine organisms during the solar eclipse of July 20, 1963. *Nature.* **205**:989–991.

BLASCO, D. 1978. Observations on the diel migration of marine dinoflagellates off the Baja California coast. *Marine Biology.* **46**:41–47.

BOWMAN, M.J., W.E. ESAIAS and M.B. SCHNITZER. 1981. Tidal stirring and the distribution of phytoplankton in Long Island and Block Island sounds. *Journal of Marine Research.* **39**:587–603.

BRIGHT, T., F. FERRARI, D. MARTIN and G.A. FRANCESCHINI. 1972. Effects of a total solar eclipse on the vertical distribution of certain oceanic zooplankters. *Limnology and Oceanography.* **17**:296–302.

COLE, B.E. and J.E. CLOERN. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology — Progress Series.* **17**:15–24.

ENRIGHT, J.T. 1977. Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. *Limnology and Oceanography.* **22**:856–872.

EPPLEY, R.W., O. HOLM-HANSEN and J.D.H. STRICKLAND. 1968. Some observations on the vertical migration of dinoflagellates. *Journal of Phycology.* **4**:333–340.

FALKOWSKI, P.G. 1981. Light-shade adaptation and assimilation numbers. *Journal of Plankton Research.* **3**:203–217.

FERRARI, F.D. 1976. The significance of the response of pelagic animals to solar eclipses. *Deep-Sea Research.* **23**:653–654.

FRANCESCHINI, G.A., T.J. BRIGHT, J.W. CARUTHERS, S.Z. EL-SAYED and A.C. VASTANO. 1970. Effects on migration of marine organisms in the Gulf of Mexico. *Nature.* **226**:1155–1156.

FURNAS, M.J. 1983. Community structure, biomass and productivity of size-fractionated summer phytoplankton populations in lower Narragansett Bay, Rhode Island. *Journal of Plankton Research.* **5**:637–655.

HARRIS, G.P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. *Canadian Journal of Fisheries and Aquatic Sciences.* **37**:877–900.

IGNATIADES, L. 1979. The influence of water stability on the vertical structure of a phytoplankton community. *Marine Biology.* **52**:97–104.

LANNERGREN, C. 1979. Buoyancy of natural populations of marine phytoplankton. *Marine Biology.* **54**:1–10.

LEVASSEUR, M., J.-C. THERRIAULT and L. LEGENDRE. 1983. Tidal currents, winds and the morphology of phytoplankton spatial structure. *Journal of Marine Research.* **41**:655–672.

MAPLES, R.S., J.N. BECK, D. CASSERLY, H.M. TURNER and M. VECCHIONE. 1984. An environmental assessment of selected estuarine habitats in Calcasieu Lake, Louisiana. Louisiana Department of Natural Resources, Final Report on Coastal Energy Impact Program Grant Number NA-83-AA-D-CZ025 to McNeese State University. 173 pp.

COLIVER, R.L. and A.E. WALSBY. 1984. Direct evidence for the role of light-mediated gas vesicle collapse in the buoyancy regulation of *Anabaena flos-aquae* (cyanobacteria). *Limnology and Oceanography.* **29**:879–886.

PETERSON, D.H. and J.F. FESTA. 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. *Estuarine, Coastal and Shelf Science.* **19**:563–589.

PIERRE, S. 1979. Problems of detection and interpretation of vertical migration. *Journal of Plankton Research.* **1**:29–44.

RINGELBERG, J. 1980. Introductory remarks: causal and teleological aspects of diurnal vertical migration. pp. 65–68. In W.C. Kerfoot (ed.) *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, NH. 793 pp.

RIVKIN, R.B., M.A. VOYTEK and H.H. SELIGER. 1982. Phytoplankton division rates in light-limited environments: Two adaptations. *Science.* **215**:1123–1125.

ROMAN, M.R. and K.R. TENORE. 1978. Tidal resuspension in Buzzard's Bay, Massachusetts. I. Seasonal changes in the resuspension of organic carbon and chlorophyll *a*. *Estuarine and Coastal Marine Science.* **6**:37–46.

SELLNER, K.G. 1983. Plankton productivity and biomass in a tributary of the upper Chesapeake Bay. I. Importance of size-fractionated phytoplankton productivity, biomass and species composition in carbon export. *Estuarine, Coastal and Shelf Science.* **17**:197–206.

SHERMAN, K. and K.A. HONEY. 1970. Vertical movements of zooplankton during a solar eclipse. *Nature.* **227**:1156–1158.

SINCLAIR, M., J.P. CHANUT and M. EL-SABH. 1980. Phytoplankton distributions observed during a 3½ days fixed-station in the lower St. Lawrence estuary. *Hydrobiologia.* **75**:129–147.

SKUD, B.E. 1967. Responses of marine organisms during the solar eclipse of July 1963. *Fishery Bulletin.* **66**:259–271.

STRICKLAND, J.D.H. and T.R. PARSONS. 1972. A practical handbook of seawater analysis (Second Edition). *Bulletin of the Fisheries Research Board of Canada.* **167**:1–310.

STUBBLEFIELD, C.L., C.M. LASCARA, AND M. VECCHIONE. 1984. Vertical distribution of zooplankton in a shallow turbid estuary. *Contributions in Marine Science.* **27**:93–104.

THERRIAULT, J.-C. and T. PLATT. 1978. Spatial heterogeneity of phytoplankton biomass and related factors in the near-surface waters of an exposed coastal embayment. *Limnology and Oceanography.* **23**:888–899.

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MYSIDACEA FROM CONTINENTAL SHELF WATERS OF THE NORTHWESTERN GULF OF MEXICO

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ABSTRACT

Eight species of Mysidacea were collected from continental shelf waters off Texas and Louisiana. *Siriella thompsonii, Anchialina typica, Amathimysis brattegardi, Pseudomma heardi* and *Mysidopsis furca* are recorded from the western Gulf of Mexico for the first time. Species accounts include morphological and ecological information and distribution records. A preliminary zoogeographical comparison of the mysids of the northwestern and northeastern Gulf of Mexico indicates a richer fauna in the latter area. This richer fauna appears to be due to the presence of tropical species in the offshore waters resulting from the intrusion of the Gulf Loop Current and an abundance of hard bottom communities in this part of the Gulf.

INTRODUCTION

The order Mysidacea includes small shrimp-like crustaceans which may occur in large numbers in shallow marine waters. They are important in the diets of fishes and larger shrimps, and are useful experimental organisms in toxicology studies (Mauchline 1980). Expansion of the knowledge of mysid biology in these areas has increased the need for taxonomic and distributional studies of these shrimp in coastal regions.

The shallow-water mysid fauna of the northwestern Gulf of Mexico has been investigated in several studies. Price (1982) summarized the distribution and ecology of mysids along the Texas coast. Several ecological studies in Louisiana waters have reported on a few species of this group (Perret 1971; Juneau 1975; Adkins and Bowman 1976; Tarver and Savoie 1976; Desselle, Poirrier, Rogers and Cashner 1978; Gillespie 1978). Banner (1953), Bowman (1964), Molenock (1969) and Stuck, Perry and Heard (1979b) have added to the taxonomic knowledge of coastal mysids in the northwestern Gulf. However, only three species have been recorded by two studies from the continental shelf waters of this region. Clarke (1956) reported *Promysis atlantica* W.M. Tattersall, 1923 and *Mysidopsis bigelowi* W. M. Tattersall, 1926 from plankton tows taken 16.1 km off Barataria Light, Louisiana. *Heteromysis* cf. *bredini* was

reported from the West Flower Garden Bank, a hermatypic coral community located 172 km south of Galveston, Texas (Pequegnat and Ray 1974).

This paper documents the species composition, ecology and morphology of three collections of mysids from the continental shelf waters off Texas and Louisiana. The information presented herein supplements scanty knowledge of offshore mysids in the northwestern Gulf of Mexico. In addition, a preliminary zoogeographical comparison of the mysid fauna of the northwestern and northeastern Gulf is made.

MATERIALS AND METHODS

Collections of mysids from the continental shelf waters off Texas and Louisiana were obtained from three sources. The largest collection came from a National Marine Fisheries Service (NMFS) cruise off Galveston Island, Texas in January, 1969. A transect of 27 stations (Collecting Sites 1–27) extended seaward from the coast. Samples consisted of 10-minute tows made with a benthic sampling sled (Brusher and Marullo 1970). The second mysid collection resulted from stomach analysis of selected demersal fishes (FSA) in shelf waters of the northern Gulf of Mexico (Collecting Sites 28–36) (Rogers 1977). The last collection consisted of benthic samples (Smith-McIntyre grab) taken off the Louisiana coast by personnel from Southwest Research Institute under Contract N. AA551-CT8-17 from the Bureau of Land Management (BLM) (Collecting Sites 37–38). These samples were passed through a 0.5 mm mesh screen.

Records of occurrence follow the style of Brattegard (1969). Although females with fully developed marsupia were common, no undisturbed brood pouches were found. This indicates brood pouch damage during the collection or predation. Therefore, no counts of eggs or embryos were possible. Total length measurements were made from the anterior margin of the rostral plate to the posterior margin of the telson.

Collecting sites are shown in Fig. 1 and sample source, station number, location, depth, fish species and bottom type are listed in the Appendix.

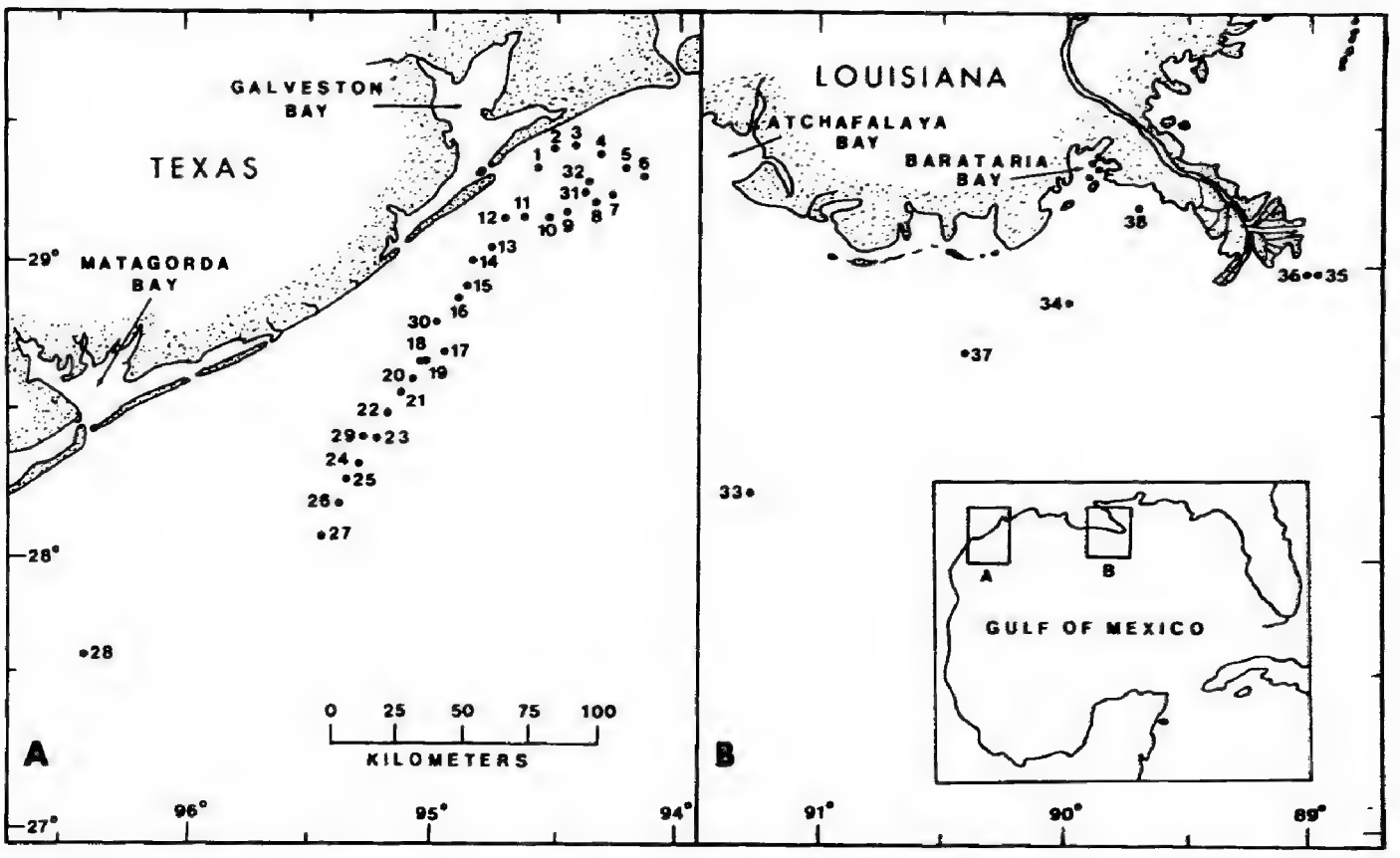

FIG. 1. Location of collecting sites in the Northwestern Gulf of Mexico.

Representative specimens of each species are deposited in the National Museum of Natural History, Smithsonian Institution and the University of Tampa Invertebrate Collection.

RESULTS

Over 3,700 mysids representing eight species were collected from 38 stations in the shelf waters off Texas and Louisiana. The occurrence, distribution, ecological and morphological notes for the species are given below.

Sirella thompsonii (H. Milne-Edwards, 1937)

Occurrence — Station 37(males – 0, immature females – 1, ovigerous females – 0, juveniles – 0).

Distribution — Oceanic and widely distributed in tropical and temperate waters of the world (Ii 1964); Gulf of Mexico (Stuck *et al.* 1979b).

Remarks — This is the second report of *S. thompsonii* from the Gulf of Mexico. Stuck *et al.* (1979b) found this species in continental shelf waters off Mississippi and Alabama. This species is generally taken near the surface and is considered a planktonic surface form. However, Tattersall (1923) and Ii (1964) documented diurnal vertical movement of *S. thompsonii.* They found that it was much more abundant in night surface collections than in daylight ones, and Tattersall concluded that it probably descends to greater depths during the day. The one specimen collected in this study was taken in a daytime grab sample at 46 m. and Stuck *et al.* (1979b) collected specimens in a daytime bottom plankton tow at 60 m. This indicates that at least a part of *S. thompsonii* populations may descend to the bottom during the day in shallow continental shelf waters.

Anchialina typica typica (Kroyer, 1861)

Occurrence — Station 25(males – 0, immature females – 1, ovigerous females – 0, juveniles – 0), 26(1-2-0-0), 28(1-1-0-0).

Distribution — Widely distributed in tropical and subtropical western Atlantic; continental shelf off northeastern Florida, South Carolina, North Carolina, Nova Scotia (Brattegard 1973); Gulf of Mexico (Tattersall 1951, Hopkins 1966, Stuck *et al.* 1979b, Stuck and Heard 1981, Modlin 1984).

Remarks — Nouvel (1971) split *A. typica* into 2 subspecies, *A. typica typica* and *A. typica orientalis*, based mainly on differences in the distal segments of the exopod of the third male pleopod. The latter subspecies has been reported from the Indian Ocean and South China Sea. Specimens from this study agreed with the description of *A. typica typica.*

Within the Gulf of Mexico *A. t. typica* has been reported from waters off Tampa Bay, Florida (Stuck and Heard 1981), the Florida Middle Ground (Modlin 1984), Cape San Blas, Florida (Tattersall 1951), St. Andrew Bay, Florida (Hopkins 1966) and the shelf waters off Mississippi, Alabama and Florida (Stuck *et al.* 1979b). This is the first report of this species from the western Gulf.

Anchialina t. typica was collected at depths of 45–59 m in this study. It has been collected on the bottom and at or near the surface in shallow and moderately shallow continental shelf waters (Tattersall 1951, Wigley and Burns 1971, Stuck *et al.* 1979b). Wigley and Burns (1971) suggested that this species may exhibit diurnal vertical movement similar to that described for *Siriella thompsonii.*

Pseudomma heardi Stuck, 1981

Occurrence — Station 29(males – 2, immature females – 1, ovigerous females – 1, juveniles – 0), 33(2-0-4-0), 35(2-0-0-0), 36a(2-0-0-0), 36b(1-0-0-0).

Distribution — Continental shelf waters off Mississippi (Stuck 1981) and Texas (present study).

Remarks — The range of *P. heardi* is extended into the northwestern Gulf of Mexico with this report. It was collected at depths ranging from 37 to 80 m. Stuck (1981) reported this species at depths of 18 to 60 m.

Body lengths ranged from 3.5 to 5.2 mm with males and females averaging 4.5 mm and 4.3 mm, respectively. The size range for ovigerous females was 3.7 to 4.5 mm.

Some morphological features in our specimens differ slightly from the original description of Stuck (1981). Specimens from our collections had more teeth (17–26, average 21.5) on the anterior and lateral margins of the ocular plate than specimens off Mississippi (16–21). The number of teeth in our specimens increased with body length. This may explain the count differences between the two collections since Stuck's largest specimens were 3.8 mm and only two of our 15 specimens were < 4.0 mm. The antennal scales of our specimens averaged 4.0 times as long as the maximum width (range 3.5–4.3) as compared to 3.8 for the Mississippi collection. This ratio increased with body length. Stuck reported that the uropodal exopod of *P. heardi* was 1.25 times as long as the endopod and 1.6 times as long as the telson. Our specimens averaged slightly lower ratios, 1.2 and 1.4, respectively, with ranges of 1.1–1.3 and 1.3–1.6, respectively.

Stuck (1981) gave no color information for his preserved *P. heardi*, but Murano (1974) noted that the body and appendages of living specimens of this genus had "more or less wine red or reddish purple" coloration. For our preserved specimens, reddish coloration was present on the following body parts: some or all thoracic legs and pleopods; the first segment of antennular peduncles and antennal scales; the proximal midventral surface of all abdominal somites; the distal ventral surface of the sixth abdominal somite; anterolateral part of carapace; bases of posterior oostegites of ovigerous females.

Amathimysis brattegardi Stuck and Heard, 1981

Occurrence — Station 19(males – 1, immature females – 0, ovigerous females – 0, juveniles – 0), 25(1-0-0-0), 27(1-0-0-0).

Distribution — Offshore of Tampa Bay, Florida (Stuck and Heard 1981) to continental shelf waters off Texas (present study).

Remarks — This is only the second record of *A. brattegardi* and extends its distribution into the western Gulf of Mexico. Stuck and Heard (1981) collected this species at depths ranging from 11 to 45 m while the three males taken in this study were found at depths of 27–51 m.

The adult males of *A. brattegardi* ranged from 2.9 to 3.6 mm in length and agree closely with the description of Stuck and Heard (1981) with some minor exceptions. They reported that the posterodorsal mucronation of the sixth abdominal segment extends over the proximal one-third of the telson. This mucronation extends one-fifth to one-third the length of the telson in our specimens. The mucronations on the posteroventral margins of the third through fifth abdominal pleura are not as pronounced in our specimens as the ones illustrated in the original description. The exopod of the uropod reported by Stuck and Heard (1981) reached two-thirds the length of the endopod. The exopods of specimens in the present study are 0.75–0.80 the length of the uropodal endopods.

Mysidopsis bigelowi W.M. Tattersall, 1926

Occurrence — Station 1(males – 12, immature females – 14, ovigerous females – 2, juveniles – 0), 2(22-36-24-2), 3(12-21-9-0), 4(30-37-11-0), 6(149-123-138-0), 7(12-8-13-0), 8(4-4-5-0), 9(17-14-12-9), 10(17-16-23-0), 11(1-0-0-0), 12(5-2-1-0), 14(191-107-105-37), 15(117-113-71-30), 16(132-83-83-0), 17(298-97-139-0), 18(79-18-76-0), 19(228-104-103-0), 20(22-11-29-0), 21(1-4-2-0), 22(1-2-0-0), 24(12-9-14-0), 26(0-2-0-0), 32a(5-8-5-0), 32b(3-4-0-0), 32c(10-0-0-0), 36b(0-0-1-0), 38(0-0-2-0).

Distribution — Georges Bank (Wigley and Burns 1971), to Pita Island, Texas (Compton 1977); Gulf of Mexico [Tattersall 1951; Clarke 1956; Bowman 1964; Brattegard 1969; Livingston, Sheridan, McLane, Lewis and Kobylinski 1977; Sheridan 1978; Stuck *et al.* 1979b; Stuck and Heard 1981; Modlin 1982; Price 1982 (summary of Texas coast localities)].

Remarks — *M. bigelowi* comprised 84% of the mysids taken in this study and is probably the most abundant mysid in the shallow to moderately shallow shelf waters in the northwestern Gulf of Mexico. It has been reported from estuaries (Hopkins 1965, Brattegard 1969, Williams 1972, Livingston *et al.* 1977, Sheridan 1978, Modlin 1982, Price 1982, Allen 1984) and offshore waters to a depth of 179 m (Wigley and Burns 1971, Stuck *et al.* 1979b, Price 1982, Allen 1984). Wigley and Burns (1971) and Stuck *et al.* (1979b) reported largest numbers of *M. bigelowi* in shelf waters with depths of 80 m or less. In the present study, it was collected in depths ranging from 7 to 47 m with greatest abundances between 18 and 27 m. The large numbers of *M. bigelowi* taken in the January NMFS samples may be partially attributed to an offshore movement of this species from northern Texas bays. Price (1976) and Allen (1984) suggested this explanation to account for decreases in *M. bigelowi* populations during the late fall-spring in Texas and New Jersey estuaries, respectively.

Price (1982) reported variation in the morphology of the endopod of the second thoracic leg of mature males between estuarine and offshore populations of *M. bigelowi* near Galveston Island, Texas. The offshore samples, collected in summer at depths of 9.2–12.2 m, were composed of offshore morphs only. The winter NMFS samples yielded both morphs at stations 1–3, the estuarine morph only at Station 9 and the offshore morph only at all other stations. This provides further evidence for the seasonal estuarine-offshore movements of *M. bigelowi*. The winter offshore movement of estuarine populations along the northern Texas coast appears to be limited to the shallow (≤ 15m) shelf waters.

The male/female ratio of 0.81 for *M. bigelowi* was similar to those reported by Price (1982) and Allen (1984), but differed from the 1.6 ratio found by Wigley and Burns (1971). Ovigerous females composed 27% of the January NMFS collections of *M. bigelowi*. In West Bay, Galveston Bay system, Texas, breeding females were found during all seasons with the greatest percentages (23–32%) recorded in the summer and fall (Price 1982). This indicates that reproduction of this species may occur at a substantial level throughout the year in the northwestern Gulf of Mexico. Ovigerous females were collected from February–November in North Carolina estuaries (Williams 1972) and from April–November in Indian River Inlet, Delaware (Hopkins 1965) and Hereford Inlet, New Jersey (Allen 1984).

Mysidopsis furca Bowman, 1957

Occurrence — Station 2(males – 0, immature females – 1, ovigerous females – 0, juveniles – 0), 14(0-1-0-0), 15(0-1-0-0), 16(9-11-0-0), 17(3-6-1-0), 18(28-1-5-0), 19(111-86-23-0), 20(9-37-6-0), 21(28-23-5-0), 22(8-5-0-0), 24(0-1-0-0), 25(8-7-1-0), 26(1-1-0-0), 27(0-1-1-0), 29(2-1-1-0), 30(1-0-0-0), 34(21-18-15-3), 36a(2-0-2-0), 36b(1-1-0-0).

Distribution — Off North Inlet, South Carolina (Bowman 1957) to continental shelf waters off Texas (present study); Gulf of Mexico (Brattegard 1969, Stuck *et al.* 1979b, Stuck and Heard 1981).

Remarks — In the Gulf of Mexico, *M. furca* has been reported from shelf waters off Mississippi and Florida (Stuck *et al.* 1979b, Stuck and Heard 1981) and Pigeon Key, Florida (Brattegard 1969). This report extends its known range into the western Gulf. This species has been reported from inshore areas and offshore waters to a depth of 48 m (Brattegard 1969). In the present study, *M. furca* was collected at depths of 7 to 51 m, but was most abundant between 18 and 45 m.

The male/female ratio for *M. furca* in all collections was 0.89. Ovigerous females composed only 10% of the January NMFS collections, but 27% of the FSA samples which were taken in June. Although this species may reproduce throughout the year in the northwestern Gulf, greatest activity appears to occur in the warmer months. Brattegard (1969) collected ovigerous females in January and February in southern Florida.

Promysis atlantica W.M. Tattersall, 1923

Occurrence — Station 16(males – 0, immature females – 0, ovigerous females – 1, juveniles – 0), 17(1-0-0-0), 19(2-0-5-0), 20(1-0-0-0), 21(1-0-0-0), 25(0-0-2-0), 26(1-1-0-0), 27(0-1-1-0), 31(4-0-1-0), 32a(4-0-1-0), 32c(8-1-10-0).

Distribution — Brazil (W.M. Tattersall 1923) to just north of Cape Hatteras, North Carolina (Wigley and Burns 1971); Gulf of Mexico [Clarke 1956, Hopkins 1966, Stuck *et al.* 1979b, Price 1982 (summary of Texas localities).]

Remarks — *P. atlantica* is a planktonic species common in tidal passes and shallow (≤ 20 m) offshore waters of the northern Gulf of Mexico (Stuck, K.C. personal communication) although it has been reported from depths greater than 100 m (Stuck *et al.* 1979b). This species was taken in depths ranging from 17 to 51 m in the present study.

Nine of the 17 specimens from the January NMFS samples were ovigerous females, indicating reproduction during the winter months. Williams (1972) collected ovigerous females of *P. atlantica* in all months except February and March along the North Carolina coast.

Brasilomysis castroi Bacescu, 1968

Occurrence — Station 14(males – 1, immature females – 0, ovigerous females – 0, juveniles – 0), 17(3-1-0-0), 32a(3-0-1-0), 32c(1-1-0-0), 36b(1-0-0-0).

Distribution — Brazil (Bacescu 1968) to Georgia (Brattegard 1974b, Stuck *et al.* 1979b); Gulf of Mexico [Brattegard 1969, Stuck *et al.* 1979b, Price 1982 (summary of Texas localities)].

Remarks — *B. castroi* is a shallow shelf species that has been reported from inshore localities (Brattegard 1969, 1973, 1974b; Price 1976) and offshore waters as deep as 40 m. (Stuck *et al.* 1979b). This species was taken in depths of 18 to 37 m in this study.

The endopod of the uropod of *B. castroi* is armed with a minute spine on the inner margin just distal to the statocyst on all specimens examined. The spine has been found on a majority of *B. castroi* from inshore waters of the Texas coast (Price 1982), but is generally absent from specimens from Brazil (Bacescu 1968), the Caribbean coasts of Colombia, Panama and southwestern Florida (Brattegard 1969, 1973, 1974a,b) and shelf waters off Mississippi (Stuck, Perry and Heard 1979a).

DISCUSSION

The northeastern (NE) Gulf of Mexico contains a richer fish (Briggs 1974) and crab (Powers 1977) fauna than the northwestern (NW) Gulf. Briggs (1958) suggested that this inequity for fishes may be due to a difference in the types of bottom communities in the two areas. A broad limestone based continental shelf west of Florida harbors a considerable hard bottom community in which a number of eurythermal tropical fish species reside. In contrast, the soft bottom shrimp ground community dominates the NW Gulf, with few hard bottom areas present.

A zoogeographical comparison of the mysid fauna from the NW and NE Gulf can only be tentative due to the paucity of collections in offshore waters, especially in the NW Gulf. The information added by the present study is from a relatively small number of collections, taken in a restricted area, mainly during one season of the year. Seasonal changes in abundance and distribution of mysids resulting from population dynamics and migration may influence interpretations of species numbers in different parts of the Gulf. However, some preliminary observations can be made.

Twenty-nine species of mysids are known from the continental shelf and inshore waters of the northern Gulf of Mexico (Stuck *et al.* 1979b, Price 1982, Modlin 1984) — 16 from the NW Gulf and 28 from the NE Gulf (Table 1). Fifteen species (52%) are common to both areas. Only *Heteromysis* cf. *bredini* has been reported from the NW but not the NE Gulf.

All 10 inshore or inshore/offshore mysid species reported from the northern Gulf are found in the western or eastern areas. It is the continental shelf component of the mysid fauna that appears to be richer in the east than the west. Of the 19 strictly offshore species in the northern Gulf, six are from the west and 18 from the east. Five (26%) are common to both areas. Of the 13 species reported only from the shelf waters of the NE Gulf, seven have tropical distributions (Caribbean Sea, Bahama Islands), three have distributions that range from the Gulf northward and three are newly described (Modlin 1984). Because all newly described species were associated with sponges, corals or an artificial habitat, they may well have tropical distributions.

The higher diversity of mysid species in the shelf waters of the NE Gulf appears to be due to the presence of tropical species. This tropical influence results from at least two factors. First, the intrusion of the Caribbean-derived Gulf Loop Current (Austin and Jones 1974) into the northern Gulf facilitates the recruitment and maintenance of tropical fauna into this area. The effects of this current have been used to explain the large tropical components of the mysid fauna (Modlin 1984) as well as other biota (Smith, Austin, Bortone, Hastings and Ogren 1975; Hopkins, Blizzard, Brawley, Earle, Grimm, Gilbert, Johnson, Livingston, Lutz, Shaw and Shaw 1977) on the Florida Middle Ground, a hermatypic coral reef in the NE Gulf. Stuck (1983) suggested that this current is important in determining the species composition of pelagic mysids and hyperiidean amphipods in the shelf waters of Louisiana and Mississippi. Second, hard bottom communities in the NE Gulf provide a heterogeneous habitat for those mysid genera with tropical members associated with coelenterates and sponges such as *Heteromysis* and *Mysidium.*

The lower number of mysid species in the NW Gulf may result from the weakened influence of the Gulf Loop Current in the western Gulf, although the Mexican current (Sturges and Blaha 1976, Hopkins *et al.* 1977) exerts a tropical influence in this region. The scarcity of hard bottom communities, and the lack of sampling effort are other factors to be considered. The faunal assemblages of only two offshore hard bottom communities, the West Flower Garden Bank (Bright, Tunnell, Pequegnat, Burke, Cashman, Cropper, Ray, Tressler, Teerling and Wills 1974) and Seven and One-Half Fathom Reef

TABLE 1

Distribution of mysid species in the continental shelf (s.) and inshore (i.) waters of the northern Gulf of Mexico.

Species	NW Gulf	NE Gulf	Distribution
Siriella chierchiae		X	s.
S. thompsonii	X	X	s.
Bowmaniella bacescui		X	s.
B. brasiliensis	X	X	i.
B. floridana	X	X	i.
B. portoricensis		X	s.
B. sewelli		X	s.
Anchialina typica typica	X	X	s.
Erythrops parva		X	s.
Pseudomma heardi	X	X	s.
Amathimysis brattegardi	X	X	s.
A. gibba		X	s.
Mysidopsis almyra	X	X	i.
M. bahia	X	X	i.
M. bigelowi	X	X	i.,s.
M. furca	X	X	s.
Metamysidopsis swifti	X	X	i.
Promysis atlantica	X	X	i.,s.
Bathymysis renoculata		X	s.
Brasilomysis castroi	X	X	i.,s.
Mysidium integrum		X	s.
Taphromysis bowmani	X	X	i.
T. louisianae	X	X	i.
Heteromysis beetoni		X	s.
H. cf. *bredeni*	X		s.
H. filitelsona		X	s.
H. formosa		X	s.
H. guitari		X	s.
H. hopkinsi		X	s.

(Felder and Chaney 1979), have been studied. Neither has been sampled systematically for mysids. Adequate sampling in these and other areas of the

northern Gulf is needed before the validity of the apparent disparity in mysid species richness between these two Gulf regions can be determined.

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LITERATURE CITED

ADKINS, G. and P. BOWMAN. 1976. A study of the fauna in dredged canals of coastal Louisiana. *Technical Bulletin. Louisiana Wildlife and Fisheries Commission.* **18**:1–72.

ALLEN, D.M. 1984. Population dynamics of the mysid shrimp *Mysidopsis bigelowi*, W.M. Tattersall in a temperate estuary. *Journal of Crustacean Biology.* **4(1)**:25–34.

AUSTIN, H. and J.I. JONES. 1974. Seasonal variation of physical parameters on the Florida Middle Ground and their relation to zooplankton biomass on the West Florida Shelf. *Florida Scientist.* **37(1)**:16–32.

BACESCU, M. 1968. *Afromysis guinesis* n.sp. and *Brasilomysis castroi* n.g.n.sp. from the waters of the tropical Atlantic. *Revue Roumaine de Biologie. Serie de Zoologie.* **13**(2):75–86.

BANNER, A.H. 1953. On a new genus and species of mysid from southern Louisiana (Crustacea: Malacostraca). *Tulane Studies in Zoology.* **1**:3–8.

BOWMAN, T.E. 1957. A new species of *Mysidopsis* (Crustacea: Mysidacea) from the southeastern coast of the United States. *Proceedings of the U.S. National Museum.* **107(3378)**:1–7.

_____. 1964. *Mysidopsis almyra*, a new estuarine mysid crustacean from Louisiana and Florida. *Tulane Studies in Zoology.* **12(1)**:15–18.

BRATTEGARD, M.T. 1969. Marine biological investigations in the Bahamas. 10. Mysidacea from shallow water in the Bahamas and Southern Florida. Part 1. *Sarsia.* **39**:17–106.

_____. 1973. Mysidacea from shallow water on the Caribbean coast of Colombia. *Sarsia.* **54**:1–66.

_____. 1974a. Additional Mysidacea from shallow water on the Caribbean coast of Colombia. *Sarsia.* **57**:47–86.

_____. 1974b. Mysidacea from shallow water on the Caribbean coast of Panama. *Sarsia.* **57**:87–108.

BRIGGS, J.C. 1958. A list of Florida fishes and their distribution. *Bulletin of the Florida State Museum. Biological Sciences.* **2(8)**:223–318.

_____. 1974. *Marine Zoogeography.* McGraw-Hill, New York. 475 p.

BRIGHT, T.J., J.W. TUNNELL, L.H. PEQUEGNAT, T.E. BURKE, C.W. CASHMAN, D.A. CROPPER, J.P. RAY, R.C. TRESSLAR, J. TEERLING and J.B. WILLS. 1974. Biotic zonation, pp. 4–54. In T.J. Bright and L.H. Pequegnat (eds.) *Biota of the West Flower Garden Bank.* Gulf Publishing Co., Houston.

BRUSHER. H.A. and F. MARULLO. 1970. Special report: a modified benthic sampling sled. Annual Report, Fiscal Year 1969, Galveston Laboratory. *U.S. Fish and Wildlife Service. Circular.* **343**:37–39.

CLARKE, W.D. 1956. Further description of *Promysis atlantica* Tattersall (Crustacea, Mysidacea). *American Museum Novitates.* **1755**:1–5.

COMPTON, C.E. 1977. A study of the mysidacean fauna of the Upper Laguna Madre. M.S. Thesis, Texas A&I University, Kingsville.

DESSELLE, P.J., M.A. POIRRIER, J.S. ROGERS and R.C. CASHNER. 1978. A discriminant functions analysis of sunfish (*Lepomis*) food habits and feeding niche segregation in the Lake Pontchartrain, Louisiana estuary. *Transactions of the American Fishery Society.* **107(5)**:713–719.

FELDER, D.L. and A.H. CHANEY. 1979. Decapod crustacean fauna of Seven and One-Half Fathom Reef, Texas: species composition, abundance, and species diversity. *Contributions in Marine Science.* **22**:1–29.

GILLESPIE, M.C. 1978. A study of Louisiana's major estuaries and adjacent offshore waters. Section II. Zooplankton analysis. *Technical Bulletin. Louisiana Wildlife and Fisheries Commission.* **27**:27–80.

HOPKINS, T.L. 1965. Mysid shrimp abundance in surface waters of Indian River Inlet, Delaware. *Chesapeake Science.* **6**:86–91.

_____. 1966. The plankton of the St. Andrew Bay system, Florida. *Publications of the Institute of Marine Science, University of Texas.* **11**:12–64.

HOPKINS, T.S., D.R. BLIZZARD, S.A. BRAWLEY, S.A. EARLE, D.E. GRIMM, D.K. GILBERT, P.G. JOHNSON, E.H. LIVINGSTON, C.H. LUTZ, J.K. SHAW and B.B. SHAW. 1977. A preliminary characterization of the biotic components of composite strip transects on the Florida Middle Ground, northeastern Gulf of Mexico. *Proceedings of the Third International Coral Reef Symposium.* pp. 31–37. Rosenstiel School of Marine and Atmospheric Science. University of Miami.

II, N. 1964. *Mysidae (Crustacea). Fauna Japonica.* Biogeographical Society of Japan. Tokyo. 610 p.

JUNEAU, C.L. 1975. An inventory and study of the Vermilion Bay Atchafalaya Bay complex. Phase II. Biology. *Technical Bulletin. Louisiana Wildlife and Fisheries Commission.* **13**:21–74.

LIVINGSTON, R.J., P.F. SHERIDAN, B.G. MCLANE, F.G. LEWIS,III and G.G. KOBYLINSKI. 1977. The biota of the Apalachicola Bay system: Functional relationships. *Florida Marine Research Publication* **26**:75–100.

MAUCHLINE, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biology.* **18**:1–369.

MODLIN, R.F. 1982. Contributions to the ecology of the mysid crustaceans in the shallow waters of Dauphin Island, Alabama. *Northeast Gulf Science.* **5**:45–49.

_____. 1984. Mysidacea from the Florida Middle Ground, northeast Gulf of Mexico, with descriptions of three new species of *Heteromysis* and a key to the Heteromysini of the western Atlantic. *Journal of Crustacean Biology.* **4(2)**:278–297.

MOLENOCK, J. 1969. *Mysidopsis bahia*, a new species of mysid (Crustacea:Mysidacea) from Galveston Bay, Texas. *Tulane Studies in Zoology and Botany.* **15(3)**:113–116.

MURANO, M. 1974. Mysidacea from the central and western Pacific. I. Genus *Pseudomma* (Tribe Erythropini). *Publications of the Seto Marine Biological Laboratory.* **21(5)**:287–334.

NOUVEL. H. 1971. Mysidacés recoltés par S. Frontier a Nosy Bé. VI. *Anchialina typica* (Kroyer) avec distinction de deux soux-especes, et *Anchialina latifrons* n. sp. *Bulletin. Societe d'Histoire Naturelle de Toulouse.* **107**:325–338.

PEQUEGNAT, L.H. and J.P. RAY. 1974. Crustaceans and other arthropods. pp. 231–288. In T.J. Bright and L.H. Pequegnat (eds.) *Biota of the West Flower Garden Bank.* Gulf Publishing Company, Houston.

PERRET, W.S. 1971. *Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana. Phase IV, Biology.* Louisiana Wildlife and Fisheries Commission. pp. 33–175.

POWERS, L.W. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. *Contributions in Marine Science.* **20 (Supplement)**:1–190.

PRICE, W.W. 1976. The abundance and distribution of Mysidacea in the shallow waters of Galveston Island, Texas. Ph.D. Dissertation, Texas A&M University, College Station.

_____. 1982. Key to the shallow water Mysidacea of the Texas coast with notes on their ecology. *Hydrobiologia.* **93**:9–21.

ROGERS, R.M. 1977. Trophic interrelationships of selected fishes on the continental shelf of the northern Gulf of Mexico. Ph.D. Dissertation, Texas A&M University, College Station.

SHERIDAN, P.F. 1978. Food habits of the bay anchovy, *Anchoa mitchilli*, in Apalachicola Bay, Florida. *Northeast Gulf Science* **2(2)**:126–132.

SMITH, G.B., H.M. AUSTIN, S.A. BORTONE, R.W. HASTINGS, and L.H. OGREN. 1975. Fishes of the Florida Middle Ground with comments on ecology and zoogeography. *Florida Marine Research Publications.* **9**:1–14.

STUCK, K.C. 1981. *Pseudomma heardi*, a new peracarid (Crustacea: Mysidacea) from continental shelf waters off Mississippi. *Gulf Research Reports.* **7(1)**:53–57.

_____. 1983. Observations on the distribution of pelagic Peracarida in the northern Gulf of Mexico (Abs.) Association of Southeastern Biologists. **30(2)**:85.

_____, H.M. PERRY and R.W. HEARD. 1979a. An annotated key to the Mysidacea of the north central Gulf of Mexico. *Gulf Research Reports.* **6(3)**:225–238.

_____, _____ and _____. 1979b. Records and range extensions of Mysidacea from coastal and shelf waters of the eastern Gulf of Mexico. *Gulf Research Reports.* **6(3)**:239–248.

_____ and R.W. HEARD. 1981. *Amathimysis brattegardi*, a new peracarid (Crustacea: Mysidacea) from continental shelf waters off Tampa Bay, Florida. *Journal of Crustacean Biology.* **1(2)**:272–278.

STURGES, W. and J.P. BLAHA. 1976. A western boundary current in the Gulf of Mexico. *Science.* **192**:367/-369.

TARVER, J.W. and L.B. SAVOIE. 1976. An inventory and study of the Lake Pontchartrain–Lake Maurepas estuarine complex. Phase II. Biology. *Technical Bulletin. Louisiana Wildlife and Fisheries Commission.* **19**:7–99.

TATTERSALL, W.M. 1923. Crustacea. Part VII: Mysidacea British Antarctic ("Terra Nova") Expedition. 1910. *Natural History Reports. Zoology.* **3(10)**:273–304.

_____. 1951. A review of the Mysidacea of the United States National Museum. *Bulletin. U.S. National Museum.* **201**:1–292.

WIGLEY, R.L. and B.R. BURNS. 1971. Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the United States in the NMFS Woods Hole collection. *Fishery Bulletin.* **69(4)**:717–746.

WILLIAMS, A.B. 1972. A ten year study of meroplankton in North Carolina estuaries: mysid shrimps. *Chesapeake Science.* **13(4)**:254–262.

APPENDIX.

List of sample sources, station locations, depths, fish species and bottom types.

NMFS Samples

1. 29° 22.5' N, 94° 34.0' W; 8.2 m.
2. 29° 26.5' N, 94° 31.0' W; 7.3 m.
3. 29° 26.5' N, 94° 24.0' W; 11 m.
4. 29° 23.5' N, 94° 19.0' W; 13.7 m.
5. 29° 20.5' N, 94° 14.0' W; 14.6 m.
6. 29° 17.5' N, 94° 10.0' W; 14.6 m.
7. 29° 15.5' N, 94° 17.5' W; 14.6 m.
8. 29° 14.5' N, 95° 22.5' W; 14.6 m.
9. 29° 13.5' N, 94° 27.5' W; 14.6 m.
10. 29° 12.5'N, 94° 32.5' W; 14.6 m.

11. 29^0 11.5' N, 94^0 37.5' W; 16.5 m.

12. 29^0 10.5' N, 94^0 42.5' W; 16.5 m.

13. 29^0 05.5' N, 94^0 46.0'W; 18.3 m.

14. 29^0 01.0' N, 94^0 49.0' W; 18.3 m.

15. 28^0 56.5' N, 94^0 52.0' W; 18.3 m.

16. 28^0 52.0' N, 94^0 55.0' W; 18.3 m.

17. 28^0 42.4' N, 94^0 58.0'W; 19.2 m.

18. 28^0 38.5' N, 95^0 04.0' W; 23.8 m.

19. 28^0 38.5'N, 95^0 04.0' W; 27.4 m.

20. 28^0 34.0' N, 95^0 07.0' W; 29.3 m.

21. 28^0 29.5' N, 95^0 10.0' W; 32.9 m.

22. 28^0 24.6' N, 95^0 13.0' W; 34.8 m.

23. 28^0 20.5' N, 95^0 16.0' W; 34.8 m.

24. 28^0 16.0' N, 95^0 19.0' W; 38.4 m.

25. 28^0 11.7' N, 95^0 21.0'W; 45.7 m.

26. 28^0 07.2' N, 95^0 24.0' W; 47.6 m.

27. 28^0 02.6' N, 95^0 27.0' W; 51.2 m.

FSA Sample

28. 27^0 37.5'N, 96^0 32.7" W; 59 m; Prionotus rubio, blackfin searobin. 5 June 1971.

29. 28^0 19.0' N, 95^0 23.8' W; 38 m; Halieutichthys aculeatus, pancake batfish 4 June 1971.

30. 28^0 46.00' N, 95^0 00.5'W; 20 m; Cynoscion nothus, silver seatrout. 1 Feb. 1973.

31. 29^0 13.1'N, 94^0 26.2' W; 17 m; Centropristis philadelphica, rock sea bass. 14 July 1971.

32. 29^0 14.2' N, 94^0 25.88' W; 17 m; a) Citharichthyes spilopterus, bay whiff; b) Etropus crossotus, fringed flounder; c) Cynoscion nebulosus, spotted seatrout; 15 July 1971

33. 28^0 10.5' N, 91^0 20.0' W; 80 m; Prionotus rubio, blackfin searobin. 6 Feb. 1972

34. 28° 52.0' N, 89° 59.0' W; 37 m; Halieutichthys aculeatus, pancake batfish. 22 June 1972.

35. 29° 02.0' N, 88° 56.0' W; 92 m; Halieutichthys aculeatus pancake batfish, 23 June 1972.

36. 29° 02.0' N, 89° 02.0' W, 37 m; a) Lepophidium brevibarbe, short-bearded cusk-eel; b) Porichthys porosissimus, midshipman 24 June 1972.

BLM Samples

37. 28° 34' N, 90° 26' W; 46 m; silt. January, 1979.

38. 29° 12' N, 89° 44' W; 12 m; sandy silt. January, 1979.

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ABUNDANCE, AGE DISTRIBUTIONS AND GROWTH OF THE TEXAS HARD CLAM, *MERCENARIA MERCENARIA TEXANA* IN TEXAS BAYS

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ABSTRACT

The hard clam *Mercenaria mercenaria* (Linne) has been well studied; however, little information is available on *Mercenaria mercenaria texana*, the subspecies found in Texas bays. Age and growth of *Mercenaria mercenaria texana* in Christmas Bay, Texas were determined by sectioning the shell and examining annual growth bands. Christmas Bay harbors a sparse population of older clams with few under five years old. Substrate type plays an important role in distribution and growth of the bivalve. Christmas Bay clams exhibited poorer recruitment and slower first year growth than did clams from Texas bays further south. *Mercenaria mercenaria texana* shows a pattern of growth similar to that reported in the literature for hybrids of *Mercenaria mercenaria* (Linne) and *Mercenaria campechiensis* (Gmelin).

INTRODUCTION

The hard clam *Mercenaria* has the most extensive distribution of any commercially valuable clam in the United States. Two species *Mercenaria mercenaria* (Linne 1758) and *Mercenaria campechiensis* (Gmelin 1790), and a subspecies *Mercenaria mercenaria texana* (Dall 1902) occur along the Gulf Coast of the United States (Ritchie 1976). Menzel (1971) suggested that *M. mercenaria texana* is a naturally occurring hybrid of *M. mercenaria* and *M. campechiensis*. The northern hard clam, *Mercenaria mercenaria*, and the southern hard clam, *Mercenaria campechiensis*, have been well studied as shown by the extensive amount of literature on them; however, little attention has been paid to the Texas hard clam, *Mercenaria mercenaria texana*. Our principal objectives in this study were to determine abundance, size and age distribution of *M. mercenaria texana* in Christmas Bay, Texas and to compare the growth rate of these clams with those of clams from other regions of the Texas coast.

Growth of molluscs is often measured as an increase in linear shell dimension. Size frequency distributions based on height can provide useful information about the age structure of the population. However, for popula-

tions composed of older clams approaching their maximum height, size frequency distributions provide little information on growth. Also, the sporadic nature of recruitment of *M. mercenaria* makes size frequency distributions unreliable indices of growth even for the smaller size classes (Haskins 1954). Aging in *M. mercenaria* is associated with a decrease in linear shell growth rate, although considerable thickening of the shell continues. Age determinations based on shell weight can be useful in separating clams of differing ages that have reached the same linear dimension. Thus, shell weight rather than shell height may reveal more about the age range of a mature clam population (Sheldon 1967).

The existence of growth bands in the shell of *M. mercenaria* is well documented (Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Clark 1974; Cunliffe and Kennish 1974; Kennish and Olsson 1975; Kennish 1978, 1980; Lutz and Rhoads 1980; Peterson, Duncan, Summerson and Safrit 1983). The use of macroscopic growth features on the surfaces of shells for age and growth determinations is limited because of the inability to distinguish true periodic structures from random disturbance marks, such as those produced by severe storms. For populations characterized by sporadic recruitment and composed of older clams that have reached a near maximum height, studying seasonal growth bands produced by the organism as revealed in cross sections of the shells provides a more useful estimate of growth rate. Growth increments revealed in shell cross sections can range from micrometers to centimeters in width and may represent environmental periodicities ranging from hours to years (Jones 1983).

Barker (1964) established five hierarchical, cyclic groupings of growth increments in the shell of *M. mercenaria*. Among these is a first order growth layering related to an annual cycle of shell formation corresponding to the yearly cycle of temperature and salinity fluctuations. These annual bands have been used by several investigators for age and growth rate determinations. Peterson *et al.* (1983) clearly demonstrated that *M. mercenaria* from southeastern populations while showing monthly growth year round, nevertheless deposit an annual marker in the shell. Saloman and Taylor (1969) examined annual bands in the shell of *M. campechiensis* and measured the distance between these bands to determine growth rates. In this paper, we use a similar approach to obtain growth rate determinations for *M. mercenaria texana*.

METHODS

Christmas Bay Site

Christmas Bay, located in the Galveston Bay area approximately 1½ miles south of the San Luis tidal pass, is a high salinity bay with no major river input (Fig. 1). It is shallow, with a maximum depth of approximately two meters. The salinity and temperature ranges are 15‰ – 31‰ and 14° C – 34° C respectively (Fisher, McGowen, Brown and Grout 1972). The substrate of the central bay

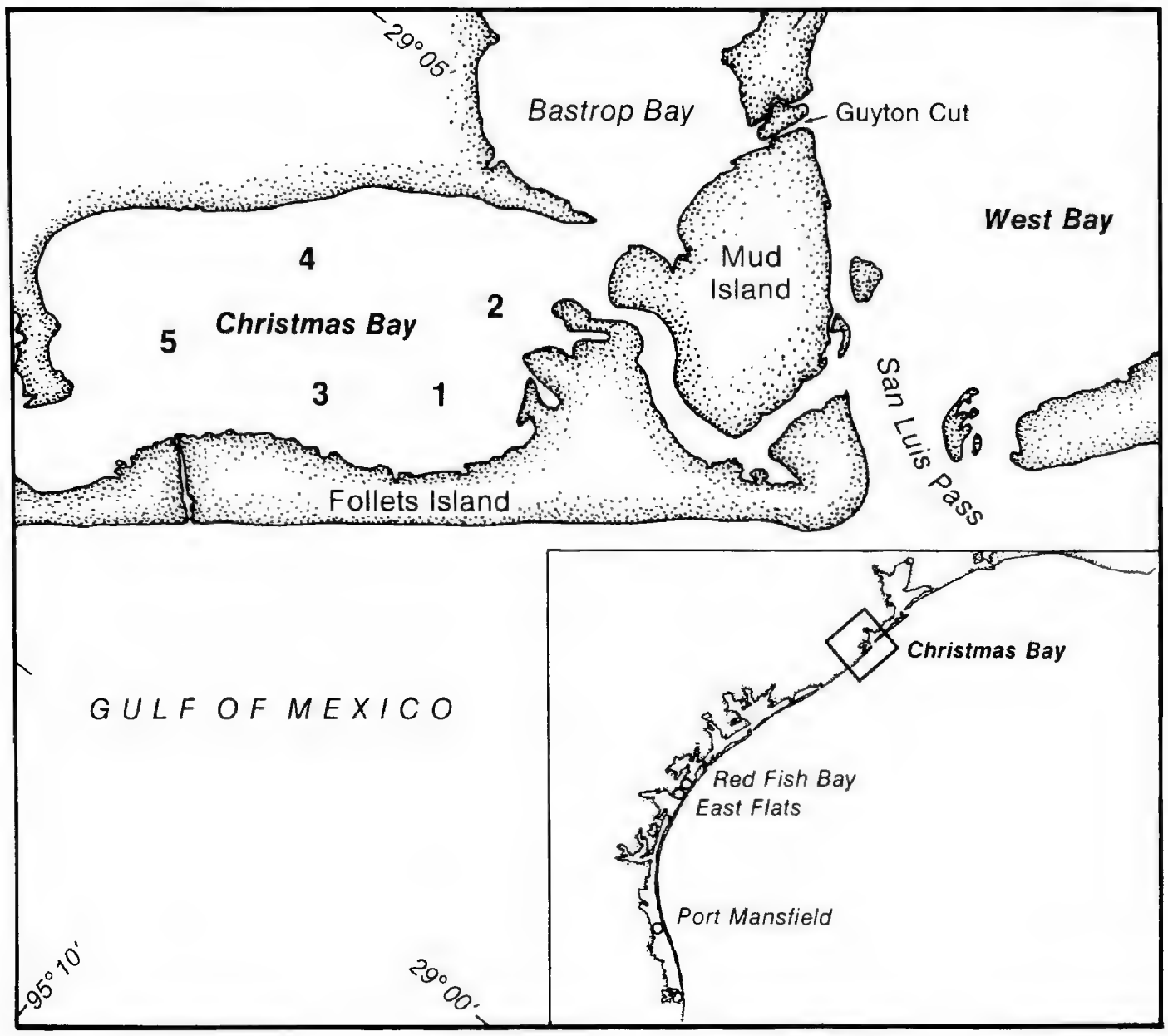

FIG. 1. Location of sample stations.

the central bay consists mostly of mud with mixed shell. The bay margins support grassflats on muddy sand and mixed shell.

Sample stations were established in five areas of Christmas Bay to assess population levels and patterns of distribution. Clam populations were initially sampled at all stations in August 1982 and then Station 3 was sampled periodically through March 1985. At each station salinity, temperature and depth were recorded and a sediment sample was taken for grain size analysis. Ten randomly chosen 5 m^2 sample units were marked off with stakes at each station. All *M. mercenaria texana* were removed from each sample unit by treading (walking repeatedly across the entire 5 m^2 area, while digging into the sediment with the feet to a depth of about 10 cm). To ensure that the smaller size classes were not being excluded by this sampling technique, samples of substrate were taken at each station and sieved. None of the smaller sized *M. mercenaria texana* were found by sieving. The number of clams present in each sample unit was recorded. Population densities were determined for each station. Height, the greatest distance from the umbo to the ventral margin, was measured on all clams found in each sample unit.

A total of 85 clams were collected from Christmas Bay between August 1982 and October 1983 and returned to the laboratory. Shell weight was measured. The shells were then sectioned and analyzed for age and growth rate analyses. Yearly growth increments were established by sectioning one valve of each shell along the greatest distance from the umbo to the ventral margin, marking off annual growth bands, and measuring the distance between successive bands to the nearest millimeter by calipers.

Ages for the clams collected were determined by counting annual bands. A statistical relationship between age and shell weight was determined through regression analysis of 184 clams collected from all areas. This relationship was used to estimate ages for older clams in which the number of annual bands in the shell was difficult to distinguish.

Other Sites

To compare growth rates of hard clams from different bays, *M. mercenaria texana* were collected from three other bays along the Texas coast (Fig. 1). Live clams were collected from East Flats, Corpus Christi Bay, from Redfish Bay, and from Port Mansfield. Redfish Bay and East Flats are located near the Aransas tidal pass and are characterized as seasonally hypersaline. The salinity range is 10‰ – 45‰ (Brown, Brewton, McGowen, Evans, Fisher and Grout 1976). Both sites have minimal river input. East Flats is a shallow sand flat, approximately ½ meter deep with a firm sandy substrate. The Redfish Bay site has a substrate of mud and sand mixed with shell. The Port Mansfield site is characterized as a restricted, seasonally hypersaline lagoon. The sample site is influenced by tidal flow from the Port Mansfield channel. Reported salinities range from 25‰ to 35‰ (Brown *et al.* 1976). All three sites have locally abundant *Diplanthera* and *Thalassia* seagrass populations which are much denser than those in Christmas Bay. Age and growth rate determinations followed the procedures used for Christmas Bay.

RESULTS

Christmas Bay

Salinity and temperature data collected for Christmas Bay show a range of 14‰ to 32‰ and 14° C to 33° C and follow the seasonal trends reported for Christmas Bay by McEachron, Shaw, and Moffett (1977) and Martinez (1974, 1975). Sediments were divided into three fractions for grain size analysis: gravel, sand and silt-clay. Stations 1, 2, 4 and 5 were predominantly sand (97.7% sand, 2.3% silt-clay). Station 3 differed due to the larger percentage of gravel (shell fragments) and the greater percent of silt-clay (38% gravel, 40% sand, 22% silt-clay).

Clam population densities, clam height ranges, and mean heights for each station (Table 1) were analyzed for significant differences by one one-way Analysis of Variance (ANOVA) and Scheffe's tests ($\alpha = 0.05$). Station 3 clams were significantly more abundant and smaller than similar aged clams from other stations. No statistical differences were detected among abundances or sizes at Stations 1, 2, 4 or 5.

A height frequency distribution for Christmas Bay clams measured during August 1982 shows a distinct absence of smaller size classes (Fig. 2) Heights ranged from 48.7 to 137 mm, with only one clam out of 225 measuring under 50 mm. Between October 1982 and October 1983 an additional 184 clams, taken primarily from Station 3 were measured. No clams under 80 mm were found and no changes in size frequency distribution were evident. In March 1985 several smaller size clams (50–60 mm) were found adjacent to the shore near Station 3.

Most of the clams in Christmas Bay have reached the age where annual increases in shell height are small. Sheldon (1967) showed that, whereas the

TABLE 1

Mean abundances and clam heights with standard deviations in parentheses for Christmas Bay Stations (August 1982).

Station	Abundance* (#clams/5m^2)		Height (mm)		
	mean	range	mean	range	N
1	1.2 (1.13)	0-3	110.1 (9.20)	96.3-126.5	12
2	1.0 (1.49)	0-4	109.2 (5.49)	100.4-117.3	10
3	18.4 (5.87	12-28	103.4 (5.87)	84.0-137.0	184
4	2.0 (1.58)	0-4	107.3 (6.79)	95.2-116.6	9
5	1.0 (1.05)	0-3	112.5 (23.76)	48.7-131.9	10

* Each station comprised 10 sample quadrats (N=10), except Station 4 which had only 5 sample quadrats (N=5). Each quadrat measured 5m^2.

rate of increase in shell height for *M. mercenaria* slows with advancing age, considerable thickening of the shell continues, indicating shell weight rather than shell height is a more reliable indicator of age in older clams. We found a similar relationship for *M. mercenaria texana* (Fig. 3). A relationship between shell weight and age was derived by linear regression using all clams (both small and large) collected from all sites (Christmas Bay, Redfish Bay, East Flats and Port Mansfield) for which the shells were sectioned and the number of annual bands could be accurately counted. There was a high degree of correlation between the known age and weight of shells with 94.5% of the variation explained by the regression formula (Fig. 4).

Based on the regression formula given in Fig. 4, ages were then estimated from shell weights of all clams that were collected between August 1982 and March 1985. The age frequency distribution for Christmas Bay using only clams collected during 1983 (Fig. 5a) shows a distinct absence of smaller size classes. To examine the dynamics of the Christmas Bay population, a hypothetical age distribution was derived using all clams collected from Christmas Bay between August 1982 and March 1985, adjusting ages to what they would have been in 1983. The result (Fig. 5b) gives a more complete picture of the population and shows a wide range of ages with the majority of clams between 5 and 11 years of age.

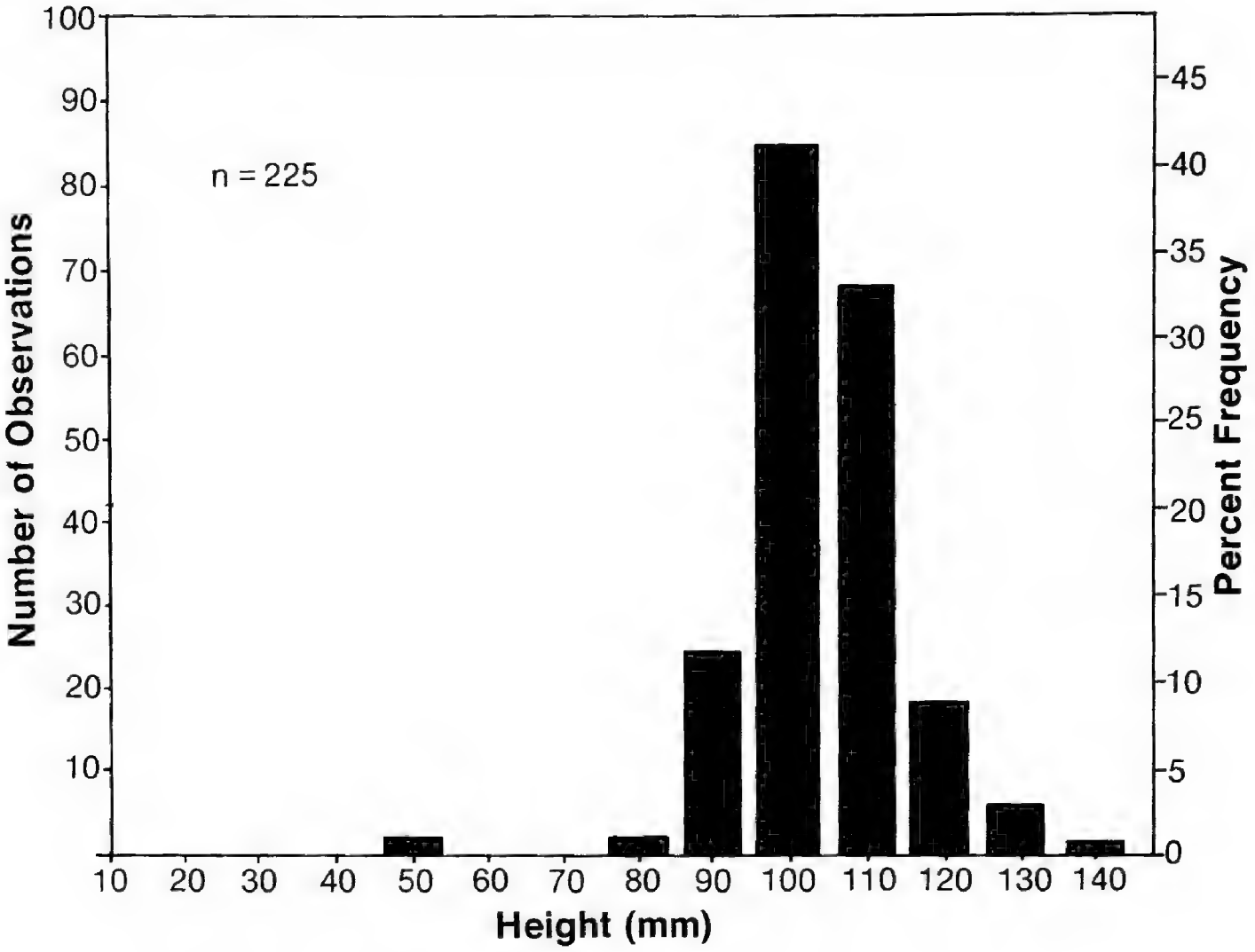

FIG. 2. Height frequency distribution for Christmas Bay (August 1982).

Mean annual growth rates (height increments) determined by reading the growth bands in shell sections for the first 5 years only (Table 2) were compared among stations. Station 3 clams showed significantly slower growth than a combination of clams from Stations 1, 2, 4 and 5 for the first, fourth and fifth years.

Other Sites

Mean annual growth rates of *M. mercenaria texana* were determined from shell sections for the first 5 years (Table 3). The growth rates from each bay were then compared using the ANOVA and Scheffe's tests. Clams from Christmas Bay showed a significantly slower growth rate for the first year and a significantly faster growth rate for the fifth year compared to the other three sites. Clams from Christmas Bay and the other bays did not differ in growth rates for the second and third year. In year 4, Christmas Bay clams showed no difference from East Flats clams but exhibited faster growth rates than clams from Redfish Bay and Port Mansfield. No statistically significant differences in growth among clams from Redfish Bay, East Flats, or Port Mansfield was found in any of the years (Fig. 6).

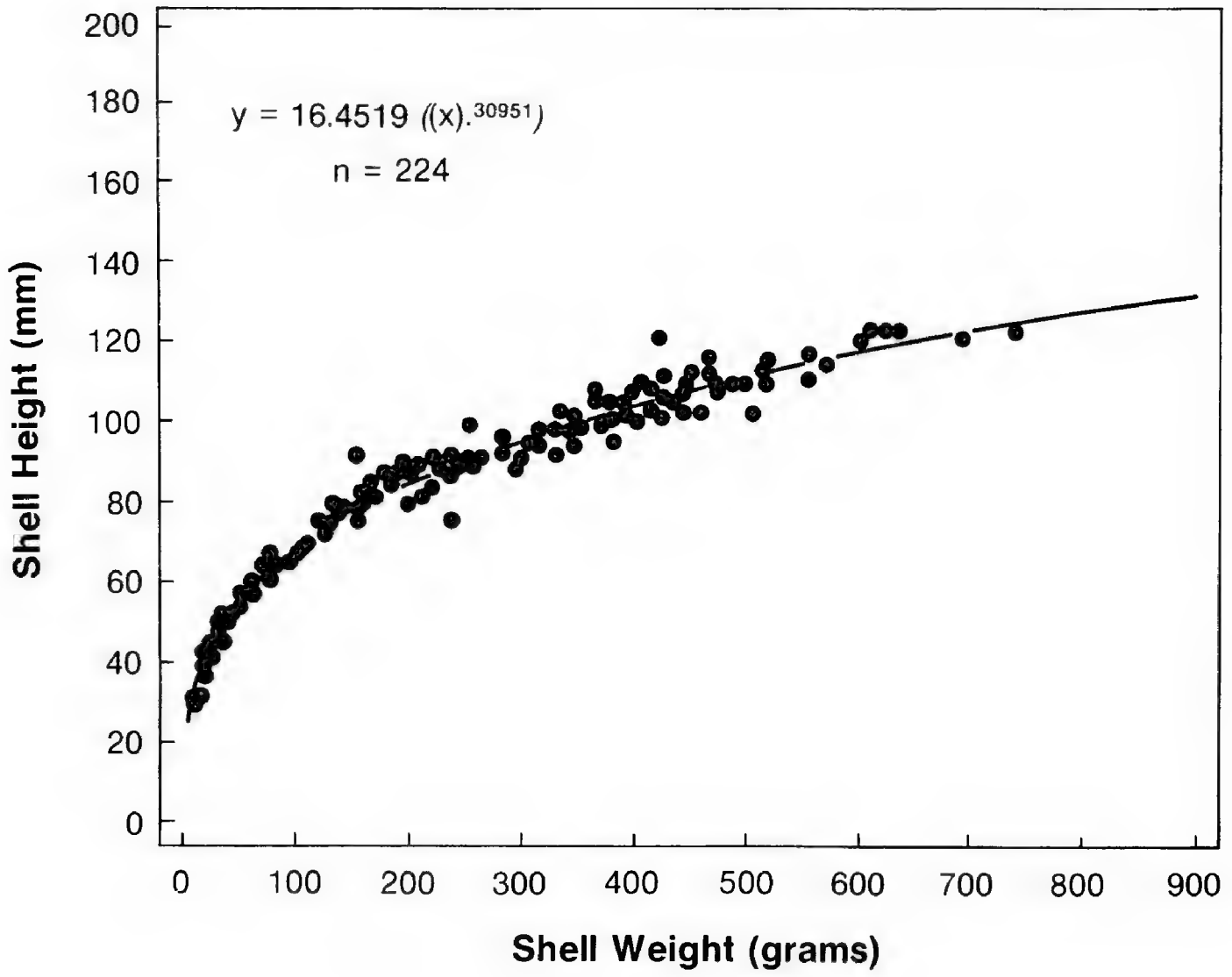

FIG. 3. Shell height to shell weight regression for *Mercenaria mercenaria texana* collected from all areas; y = shell height, x = shell weight.

DISCUSSION

Size and age frequency distributions for Christmas Bay show a population composed mostly of larger, older clams. Few small living clams were seen throughout the 28 months of sampling. Factors affecting the survival of hard clam populations include temperature and salinity, sediment composition and predation pressure (Pratt 1953, Wells 1957, Carriker 1959, Castagna and Kraeuter 1977, Arnold 1984, Walker and Tenore 1984). All three factors may contribute to the near absence of smaller size classes in Christmas Bay.

Larval sets of hard clams are naturally sporadic (Hibbert 1976). Low salinity can affect gonadal development, growth and mortality of larval, juvenile and adult clams (Burrell 1977). Embryonic stages of hard clams are not as tolerant of low salinity as are the larvae. The minimum salinity at which *M. mercenaria* larvae can survive is 15‰ (Castagna and Chanley 1973). The minimum salinity tolerance of *M. campechiensis* is not precisely known but is presumed to be higher (Menzel 1971). Although no information is available on salinity tolerances of *M. mercenaria texana*, the minimum salinities reported for Christmas Bay may be below the limit. A sporadic larval population could be responsible for the population age structure seen in

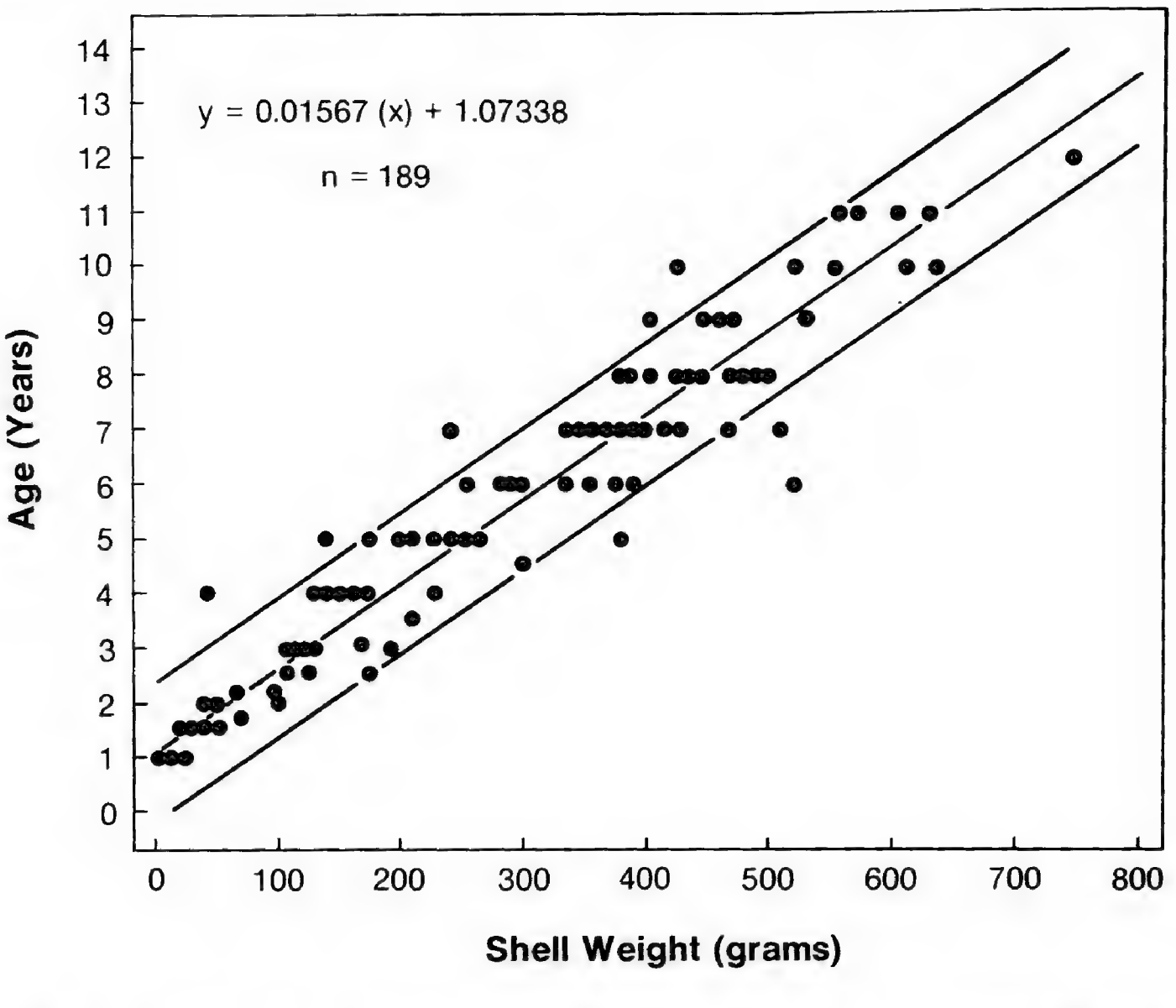

FIG. 4. Age to shell weight regression for *Mercenaria mercenaria texana* (with 95% confidence limits). Age (y) determined by counting the number of annual bands, shell weight (x) is the weight of both valves.

Christmas Bay; however, information on larval settlement and recruitment in Christmas Bay is not available.

Field studies have shown that predators, when numerous, have been responsible for removal of substantial numbers of clams, sometimes all, before the clams reach 50 mm (Menzel and Sims 1964, Castagna and Kraeuter 1977, Kraeuter and Castagna 1980, MacKenzie 1979). Hofstetter and Johnson (1965) suggested predation on juvenile clams as the limiting factor for clam populations in West Bay, Galveston, Once the clams reach a larger size, predation pressure may be less intense. Increase in clam size results in decreased mortality (Whetstone and Eversole 1978). Arnold (1984) found that hard clams over 40 mm were not consumed by blue crabs. Some predators such as whelks (*Busycon* spp.) and stone crabs (*Menippe mercenaria* may consume even large clams, but their influence on clam populations may not be as great (Peterson 1982).

The higher density of clams at the station with shell fragments in the substrate is not surprising. Pratt (1953), Wells (1957) and Walker and Tenore

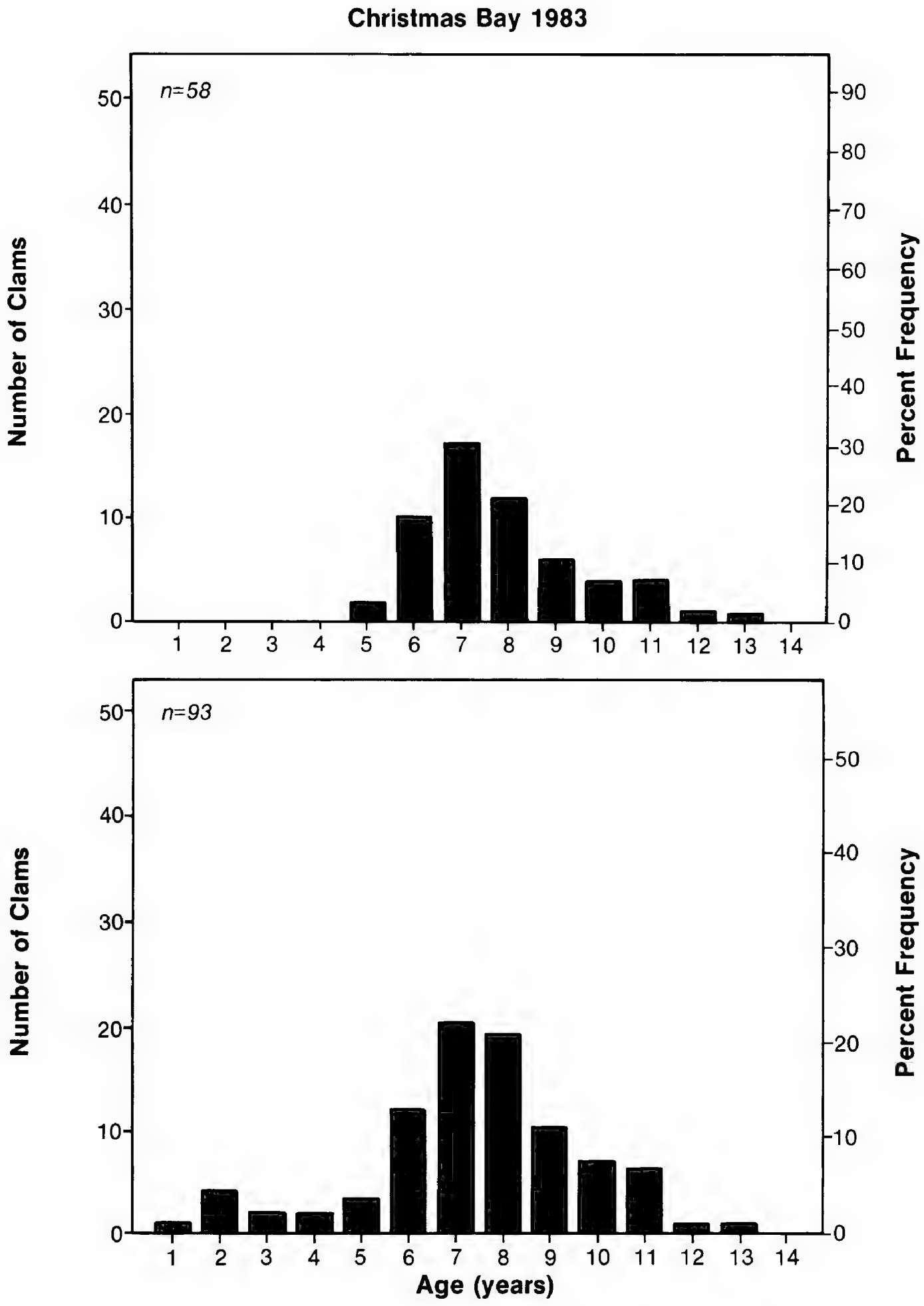

FIG. 5. Age distribution for *Mercenaria mercenaria texana* from Christmas Bay (a) for 1983 only and (b) for clams collected between August 1982 and March 1985, with their ages converted to what they would have been in 1983. Age is estimated from shell weight using $y = 0.01567(x) + 1.07338$ where y = age and x = shell weight.

TABLE 2

Mean growth rates with standard deviations in parentheses for clams from different stations in Christmas Bay. A sample of clams from Stations 1, 2, 4 and 5 was compared with a sample of clams from Station 3 using ANOVA ($\alpha = 0.05$).

	Annual Shell Height Increments (mm)				
Station	Year 1	Year 2	Year 3	Year 4	Year 5
(3) *N*=46	30.9 (3.8)	22.7 (4.0)	19.1 (3.8)	14.8 (3.3)	9.8 (3.1)
(1,2,4,5)* *N*=28	33.4 (4.3)	22.7 (4.3)	19.9 (3.9)	16.5 (3.7)	13.5 (3.0)
ANOVA**	+	-	-	+	+

* The clams from Stations 1, 2, 4 and 5 were combined for growth studies on the basis of no significant difference in clam sizes (heights) between these stations.

** A significant difference in growth (alpha = 0.05) between clams from different samples is indicated by (+). No significant difference is indicated by (-).

(1984) found *Mercenaria mercenaria* most abundant in sediments containing large particles such as shell fragments. The presence of shell may enhance population densities by reducing the loss of seed due to currents and by providing a favorable substrate to which the clam larvae can attach in the byssal stage (Wells 1957). Protection from predation may be another important benefit derived from the presence of the shell fragments. The shell fragments at Station 3 may have provided the young clams with a partial predation refuge. Arnold (1984) demonstrated that blue crabs preferred sand and mud over crushed shell when feeding. This suggests that the clams at Station 3 may be less vulnerable to predation and therefore are more abundant. The smaller size clams found in March 1985 were also found in substrate with a substantial amount of oyster shell.

Along with a greater abundance of clams, Station 3 shows somewhat smaller sizes for clams of the same age and a tendency towards slower growth. Both could be attributable to substrate characteristics. Pratt (1953) found that *M. mercenaria* grew 25% faster in sand than in mud and suggested that suspended silt reduces the pumping rate and requires the clam to

TABLE 3

Mean growth rates with standard deviations in parentheses for clams from Christmas Bay (CB), Redfish Bay (RF), East Flats (EF), and Port Mansfield (PM).

	Annual Shell Growth Increments (mm)				
Site	Year 1	Year 2	Year 3	Year 4	Year 5
CB*	30.8	23.4	19.7	15.6	11.3
N=63	(3.4)	(3.4)	(3.3)	(3.4)	(3.8)
EF	38.5	25.1	19.8	14.7	8.1
N=28	(4.4)	(6.4)	(6.1)	(5.9)	(4.0)
RF	36.1	22.7	17.1	12.1	7.2
N=18	(4.4)	(3.2)	(4.3)	(4.0)	(2.5)
PM	35.2	24.8	16.9	11.3	6.9
N=14	(7.9)	(7.4)	(5.3)	(3.3)	(2.3)
Scheffe's Groups**	CB EFRFPM	CBEFRFPM	CBEFRFPM	CBEFRFPM	CB EFRFPM

* Based on random samples of clams taken from Stations 1,2,3,4 and 5.

** Stations showing no significant difference at the alpha = 0.05 level are joined with a horizontal bar.

frequently clear its feeding apparatus, thus interfering with the feeding process. Bricelj, Malouf and Quillfeldt (1984) found high concentrations of silt-clay inhibited growth of *M. mercenaria* in soft bottoms. The higher percentage of silt at Station 3 could also indicate a slower current and thus a lower food supply. A tendency for slower growth could explain the smaller sizes found for clams from Station 3.

A comparison of Christmas Bay clams with those from other bays along the Texas Coast reveals differences in population structure and growth rates. All of the other bays had more of the smaller sizes than Christmas Bay. However, the scarcity of living clams under 30 mm at these other sites (none were collected) does indicate high mortality in the first year. The denser seagrass beds at these sites could partially explain the presence of clams 30 mm – 70 mm, which were scarce in Christmas Bay. Peterson (1982) demonstrated that the whelk, genus *Busycon*, an important predator on *M. mercenaria*, is relatively ineffective within seagrass beds. Whelks were seen preying on *M. mercenaria texana* at the Redfish Bay site and evidence of whelk predation (notches on the shell margins) could be seen in many of the clam shells collected from all three south Texas bay sites.

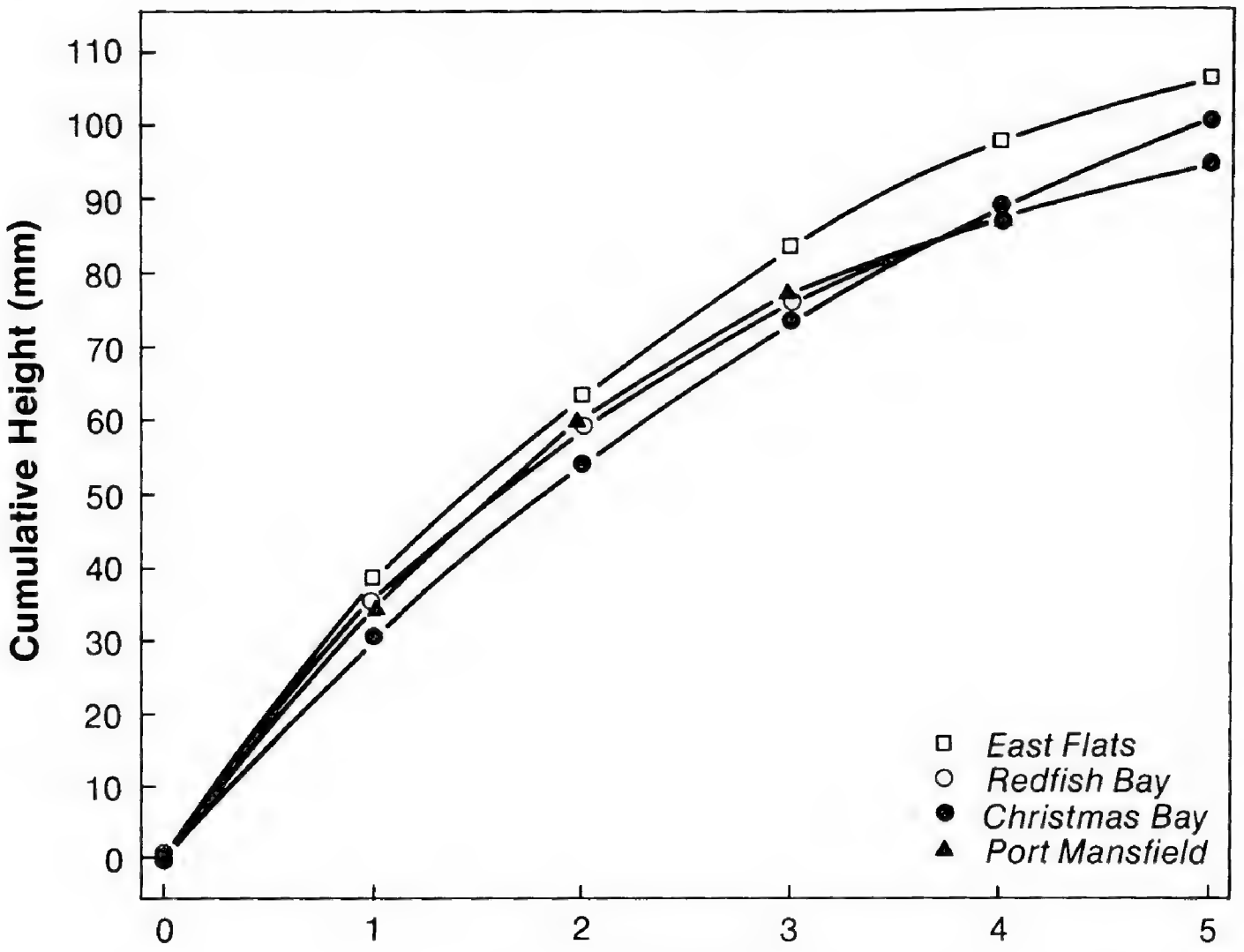

FIG. 6. A comparison of *Mercenaria mercenaria texana* growth rates between Texas bays (first 5 years only).

The higher densities of seagrass may influence growth rates of *Mercenaria mercenaria texana*. Clams from the south Texas bays show faster growth rates in the first year than those from Christmas Bay. Peterson, Summerson, and Duncan (1984) found higher growth for *M. mercenaria* in seagrass beds compared to *M. mercenaria* in sand flats and suggested that seagrass beds may be enhancing growth by increasing bottom food concentrations. Higher temperatures and salinities characteristic of the southern bays may also be contributing to the faster growth seen there.

Growth rates determined for *M. mercenaria texana* from all four bays were compared to those reported by Menzel (1971) for *M. mercenaria*, *M. campechiensis*, and hybrids of the two species. Our *M. mercenaria texana* growth rates most closely resemble those of Menzel's hybrids.

In summary, the sparse population of predominantly older clams found in Christmas Bay suggests sporadic recruitment and intense predation. Within the bay, substrate appears to play an important role in distribution and growth as seen by the higher abundances, smaller sizes and slower growth for clams from bay bottom with a substantial mixture of shell and silt. A comparison of

the clam population from Christmas Bay with clams from other bays along the Texas Coast indicates poorer recruitment and slower growth during the first year for the Christmas Bay population. The growth rates we determined for *M. mercenaria texana* were comparable to those reported in the literature for hybrids of *M. mercenaria* and *M. campechiensis*.

ACKNOWLEDGMENTS

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LITERATURE CITED

ARNOLD, W.S. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab (*Callinectes sapidus* Rathbun) on the hard clam (*Mercenaria mercenaria* Linne). *Journal of Experimental Marine Biology and Ecology.* **80(3)**:207–220.

BARKER, R.M. 1964. Microtextural variation in pelecypod shells. *Malacologia.* **2**:69–86.

BRICELJ, B.M., R.E. MALOUF and C. de QUILLFELDT. 1984. Growth of juvenile *M. mercenaria* and the affect of resuspended bottom sediments. *Marine Biology.* **84**:167–173.

BROWN, L.F., J.L. BREWTON, J.H. McGOWEN, T.J. EVANS, W.L. FISHER and C.G. GROUT. 1976. Environmental Geologic Atlas of the Texas Coastal Zone – Corpus Christi Area. Bureau of Economic Geology, University of Texas at Austin, Austin, Texas 78712.

BURRELL, VICTOR. 1977. Mortalities of oysters and hard clams associated with heavy runoff of the Santee river system, South Carolina in spring 1975. *Proceedings of the National Shellfish Association.* **67**:35–43.

CARRIKER, M.R. 1959. The role of physical and biological factors in the culture of *Crassostrea* and *Mercenaria* in a saltwater pond. *Ecological Monographs.* **29(3)**:219–266.

CASTAGNA, M.A. and P.E. CHANLEY. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. *Malacologia.* **12(1)**:47–96.

_____ and J.N. KRAEUTER. 1977. *Mercenaria* culture using stone aggregate for predator protection. *Proceedings of the National Shellfish Association.* **67**:1–6.

CLARK, G.R. 1974. Growth lines in invertebrate skeletons. *Annual Review of Earth and Planetary Sciences.* **2**:77–79.

CUNLIFFE, J.E. and M.J. KENNISH. 1974. Shell growth patterns in the hard-shelled clam. *Underwater Naturalist.* **8(4)**:20–24.

FISHER, W.L., J.H. McGOWEN, L.F. BROWN and C.G. GROUT. 1972. Environmental Geologic Atlas of the Texas Coastal Zone – Galveston/Houston Area. Bureau of Economic Geology, University of Texas at Austin, Austin, Texas 78712.

HASKINS, H.H. 1954. Age determination in mollusks. *Transactions of the New York Academy of Science.* **16(6)**:300–304.

HIBBERT, C.J. 1976. Biomass and production of a bivalve community on an intertidal mudflat. *Journal of Experimental Marine Biology and Ecology.* **25**:249–261.

HOFSTETTER, R.P. and R.B. JOHNSON. 1965. Study of the southern quahog (*Mercenaria campechiensis* Gmelin) in Texas waters. Project number MO-R-7, Jobs nos. 7 & 8.

JONES, D.S. 1983. Schlerochronology: Reading the record of the molluscan shell. *American Scientist.* **71**:384–391.

KENNISH, M.J. 1978. Effects of thermal discharges on mortality of *Mercenaria mercenaria* in Barnegat Bay, New Jersey. *Environmental Geology.* **2(4)**:223–254.

_____. 1980. Growth models of the northern quahog, *Mercenaria mercenaria* (Linne). *Proceedings of the National Shellfish Association.* **70**:230–239.

_____ and R.K. OLSSON. 1975. Effects of thermal discharge on the microstructural growth of *Mercenaria mercenaria*. *Environmental Geology.* **1**:41–64.

KRAEUTER, J.N. and M. CASTAGNA. 1980. Effects of large predators on the field culture of the hard clam, *Mercenaria mercenaria*. *Fishery Bulletin.* **78(2)**:538–541.

LUTZ, R.A. and D.C. RHOADS. 1980. Growth patterns within the molluscan shell — an overview. pp. 203–254. In D.C. Rhoads and R.A. Lutz (eds.) *Skeletal Growth of Aquatic Organisms*. Plenum Press. N.Y.

MacKENZIE, C.L. 1979. Management for increasing clam abundance. *Marine Fisheries Review*. **41(10)**:10–22.

MARTINEZ, A.R. 1974. Coastal hydrographical and meteorological study, 1974. pp. 61–108. In Coastal Fisheries Project Report 1974. Texas Parks and Wildlife Department.

_____. 1975. Coastal hydrological and meteorlogical study. pp. 100–157. In 1975 Texas Parks and Wildlife Department, Coastal Fisheries Project Report.

McEACHRON, L.W., L.R. SHAW AND A.W. MOFFETT. 1977. A fishery survey of Christmas, Drum and Bastrop Bay, Brazoria County, Texas. *Technical Series, Texas Parks and Wildlife Department. No.* **20**:1–83.

MENZEL, R.W. 1971. Quahog clams and their possible mariculture. *Proceedings of the Second Annual Workshop, World Mariculture Society.* **2**:23–36.

_____ and H.W. SIMS. 1964. Experimental farming of hard clams, *Mercenaria mercenaria*, in Florida. *Proceedings of the National Shellfish Association.* **65**:59–62.

PANNELLA, G. and C. MacCLINTOCK. 1968. Biological and environmental rhythms reflected in Molluscan shell growth. *Journal of Paleontology.* **42**:64–79.

PETERSON, C.H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Marine Biology.* **66**:159–170.

_____, P.B. DUNCAN, H.C. SUMMERSON and G.W. SAFRIT, JR. 1983. A mark-recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. *Fishery Bulletin.* **81(4)**:765–779.

_____, H.C. SUMMERSON and P.B. DUNCAN. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research.* **42(1)**:123–138.

PRATT, D.M. 1953. Abundance and growth of *Venus mercenaria* and *Callocardia morrhunana* in relation to the character of bottom sediments. *Journal of Marine Research.* **12(1)**:60–74.

RHOADS, D.C. and G. PANNELLA. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia.* **3(2)**:143–161.

RITCHIE, T.P. 1976. A comprehensive review of the commercial clam industries of the United States. U.S. Department of Commerce, NOAA, National Marine Fisheries Service (Delaware Sea Grant Program, College of Marine Studies, University of Delaware at Newark and Lewes, DE, DEL-SG-26-76), ix 106 p.

SALOMAN, C.H. and J.L. TAYLOR. 1969. Age and growth of large southern quahogs from a Florida estuary. *Proceedings of the National Shellfish Association.* **59**:46–51.

SHELDON, R.W. 1967. Relationship between shell-weight and age in certain molluscs. *Journal of the Fisheries Research Board of Canada.* **24(5)**:1165–1171.

WALKER, R.L. and R. TENORE. 1984. The distribution and production of the hard clam, *Mercenaria mercenaria* in Wassaw Sound, Georgia. *Estuaries.* **7(1)**:19–27.

WELLS, H.W. 1957. Abundance of the hard clam *Mercenaria mercenaria* in relation to environmental factors. *Ecology.* **38(1)**:123–128.

WHETSTONE, J.M. and A.G. EVERSOLE. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. *Proceedings of the National Shellfish Association.* **68**:42–48.

Contributions in Marine Science. (1986) Vol. 29:73–89.

POPULATION DYNAMICS OF AN *R*-SELECTED BIVALVE, *MULINIA LATERALIS* (SAY) IN A NORTH CAROLINA ESTUARY

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ABSTRACT

Populations of the clam *Mulinia lateralis* in a North Carolina estuary exhibited repeated seasonal changes in abundance from 1974 to 1977. Intensive sampling at five stations in different sediment regimes revealed similar patterns of density as high as 1650 m^{-2} in late winter to early spring with a steady decline during May and June to very low summer levels. Abundance increased again during mid-fall and early winter. An extended reproduction season and seasonal predatory activity appeared to be the main factors controlling these *M. lateralis* population changes. Temperatures and salinity conditions were suitable for reproduction in all seasons except winter. However, rapid cropping by predators apparently masked the actual magnitude of recruitment to these clam populations during spring and summer.

Population dynamics of *M. lateralis* in estuaries in warmer latitudes (from South Carolina to Maryland) were more periodic and persistent than descriptions of this species from colder climates, *i.e.* Long Island Sound. Geographical differences may be due to extended reproduction seasons and higher predation pressures for southern *M. lateralis* populations. The different ecological advantages of *r*-selected reproduction in this clam may vary geographically.

INTRODUCTION

Study Approach

The reproductive biology and population dynamics of the dwarf surf clam *Mulinia lateralis*, a small (usually < 2.0 cm), but prolific bivalve, were first detailed for populations living in Long Island Sound, New York (Calabrese 1969a, Levinton 1970, Levinton and Bambach 1970). Observations from benthic community analyses of Sanders (1956) and dead shell sampling

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characterized these Long Island Sound populations temporally as being extremely transient and aperiodic in occurrence (Levinton 1970, Levinton and Bambach 1970). Subsequent studies in Chesapeake Bay (Boesch 1973, Boesch, Diaz and Virnstein 1976a, Boesch, Wass and Virnstein 1976b) produced similar descriptions of *M. lateralis* abundance as being ephemeral and sporadic. However, Virnstein (1977) described *M. lateralis* populations for the same Chesapeake Bay area as displaying dense periodic eruptions in winter or early spring with high summer mortality; reducing their numbers to low density reservoir populations.

The often dramatic fluctuations in *Mulinia lateralis* abundance have been attributed to the opportunistic nature (Levinton 1970) of this *r*-selected clam. *M. lateralis* exhibited very high fecundity (Calabrese 1969a), broad habitat requirements (Breuer 1957, Tenore 1970, Parker 1975), and short generation time (Calabrese 1969a). These intrinsic qualities have apparently enabled *M. lateralis* to rapidly invade and colonize available substrate (Levinton 1970). Hypotheses for the decline and disappearance of these populations have emphasized physical causes, *e.g.* turbidity and filter clogging (Jackson 1968, Rhoads and Young 1970, Levinton 1970, Bloom, Simon and Hunter 1972, Boesch *et al.* 1976a), sediment burial (Leathem, Kinner, Maurer, Biggs and Treasure 1973), oxygen depletion (Tenore 1970) and metabolic stresses from high temperature and reduced oxygen (Shumway 1983, Shumway and Newell 1984). However, seasonal predation may be a more important factor producing spring to summer declines for many *M. lateralis* populations. Predation was cited as a dominant source of mortality for *M. lateralis* in Chesapeake Bay (Virnstein 1977; Holland, Mountford, Hiegel, Kaumeyer and Mihursky 1980) and in Texas (Dent 1983).

Mulinia lateralis extend along the Atlantic and Gulf Coasts from Canada to Mexico (Parker 1975) and occur in Texas in salinities from 1.4 to 75.1‰ (Breuer 1957). For this reason caution must be exercised in applying conclusions about factors controlling *M. lateralis* dynamics in one environment, *i.e.* Long Island Sound, to more generalized ranges. Important questions are generated by the varying descriptions (Levinton 1970, Boesch 1973, Boesch *et al.* 1976a,b, Virnstein 1977) of *M. lateralis* abundance patterns and their controlling factors within and between biogeographic regions. How do reproductive seasonality, abiotic mortality, and predation interact to control population dynamics? Within this clam's broad geographical range, might populations be persistent for some habitats and more transient in others? To what degree might observed periodicity or aperiodicity in density be a function of climate and habitat conditions or sampling methods? Our study considered these questions in developing objectives to determine (1) whether *M. lateralis* populations were highly transient and aperiodic from year to year; (2) how abundance patterns differed for different habitat conditions, *e.g.* substrate; and (3) the seasonal roles of predation and juvenile clam recruitment in controlling population changes. Study results would be important in quantifying the potential contribution of *M. lateralis* to its surrounding ecosystem.

Study Area

The lower Cape Fear River near Southport, North Carolina, USA (33° 58′ N; 77° 58′ W) (Fig. 1) is a physically dynamic, nonstratified estuary. Sixty-seven kilometers above its mouth, river discharge varies seasonally from 20.2 million m^3 day^{-1} to 128.6 million m^3 day^{-1} (Wilder 1967, summarized in Hobbie 1971). Temperature ranges from 3.0° C in winter to 31.0° in summer, while salinity can vary from 1.7 to 32.2‰, depending upon river discharge (Hobbie 1971).

Five sampling stations were located in the area of Walden Creek and Snows Marsh on the west side of the Cape Fear River about 11.7 km upriver from the mouth of the estuary. Conditions of temperature, salinity, and tidal range there were similar to conditions in the Cape Fear River. The intake canal of the Brunswick Steam Electric Plant (BSEP) is adjacent to Snows Marsh and transects the marsh and Walden Creek to reach the Cape Fear River (Fig. 1).

METHODS

Changes in *Mulinia lateralis* populations in the vicinity of Snows Marsh and Walden Creek were determined from samples collected from March 1974 to April 1977. Samples at each station were collected randomly with a Ponar grab which sampled a bottom area of 0.05 m^2 to a maximum depth of about 10 cm in soft substrate. Sediment from each grab was washed through a 1.0 mm mesh screen and *M. lateralis* were later separated from the formalin preserved samples. A smaller mesh screen was not used due to the high concentration of detritus from adjacent salt marshes.

The statistical distribution describing *Mulinia lateralis* spatial patterns at each station was determined using an index of dispersion (I) derived from the sampling variance (s^2) to mean (x) ratio ($I = s^2/x$, from Elliott 1971). A χ^2 test was used to determine if I departed from unity (Poisson distribution) at the $p = 0.05$ level of significance. Upon determining clam dispersion patterns for each station (ST1, ST2, ST3, ST4, and ST5), equations from Elliott (1971) were used to determine sample size precision. The number of grabs actually collected from each trip were 8 at ST1, 5 at ST2, 17 at ST3, 6 at ST4, and 3 at ST5.

Biweekly sampling for all stations was begun in May 1975 and continued through June 1976 for ST1, ST2, ST3, and ST4 and until mid-July for ST5. However, during December 1975 and January and February 1976, sampling intervals were lengthened to 3 weeks. ST5 was further sampled in September 1976 and February, March, and April 1977 to follow longer-term population trends.

Habitat conditions (*e.g.* substrate, phytoplankton concentrations, temperature, salinity, and current velocities) and predator abundance were measured at each station for use in analyzing differences in *Mulinia lateralis* densities between sites and the seasonal effects of predation. Sediments were sampled in June 1976 and March 1977 and analyzed using methods outlined by Buchanan and Kain (1971) to detect any long term changes in particle size composition. Sediment parameters including sorting coefficient and Folk's textural description (Folk 1968) were calculated using a computer program (provided by V. Cavaroc, personal communication). Current velocity at each station was measured using an electronic current meter at peak flood tide velocities just above the bottom. Seasonal predator abundance was determined from trawl samples taken concurrently by other researchers (Birkhead, Copeland and Hodson 1979) at adjacent sites. Additional trawl samples were collected monthly at each benthic station from March through June 1976 for length and weight measurement and stomach content analysis.

Since blue crabs, *Callinectes sapidus*, had been identified as an important predator of *Mulinia lateralis* (Tagatz 1968, Virnstein 1977) and were abundant in the study area (Birkhead *et al.* 1979), experiments were conducted to assess blue crab predation and test the hypothesis that blue crabs

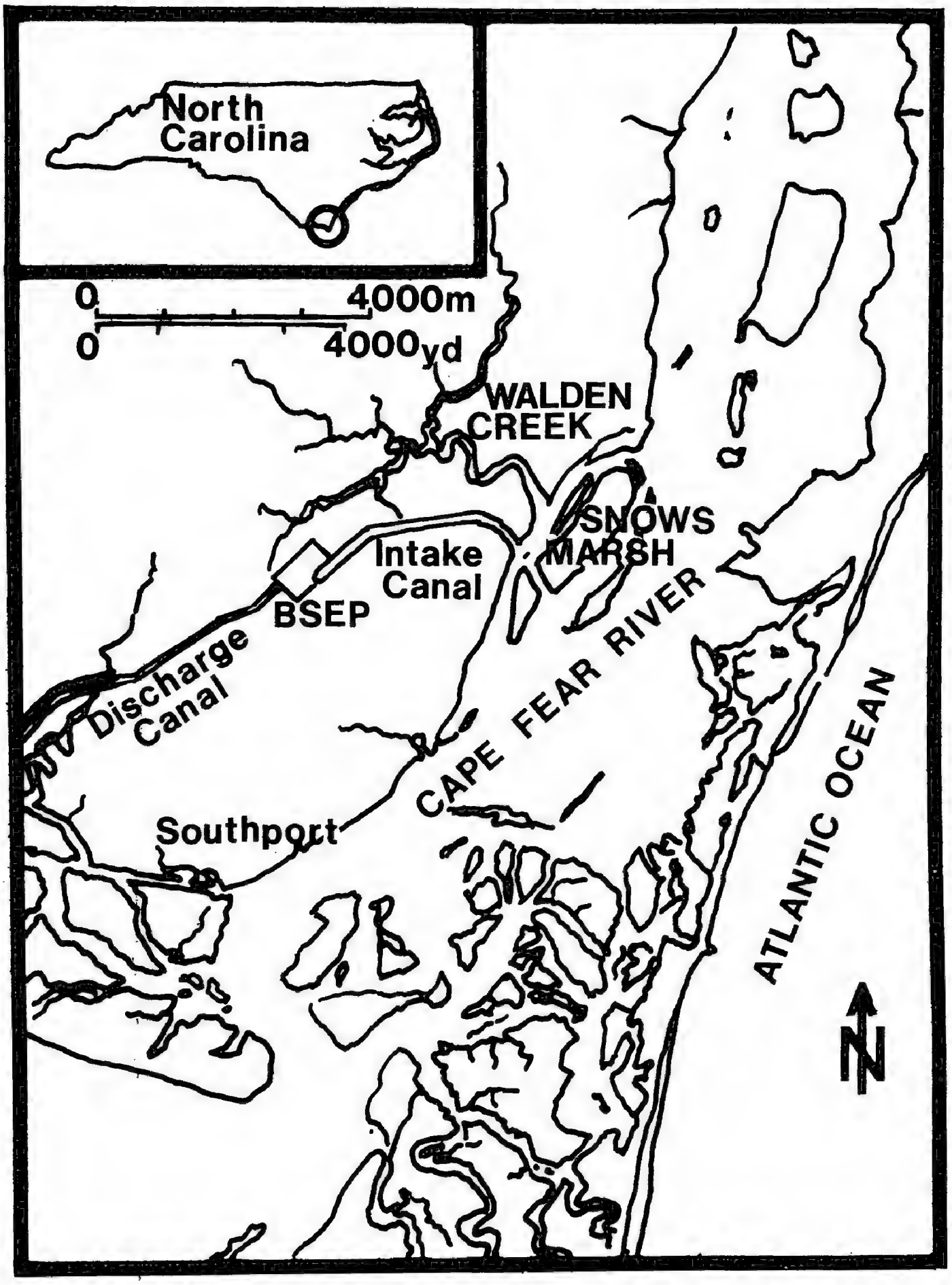

FIG. 1. Geographical location of the lower Cape Fear River estuary showing the Walden Creek and Snow's Marsh study area.

of different sizes fed differentially on clams of several sizes. Muddy sediment, sieved through a 1.0 mm mesh screen, was spread in a 3.0 cm layer in the bottom of plastic trays, 32 × 24 × 15 cm deep

(bottom = 0.08 m^2). Each tray was then filled with ambient estuarine water and 10 *M. lateralis* from 2.6 to 10.0 mm long (approximating spring length frequencies and density) were scattered upon the sediment. After the clams had burrowed or been pushed below the sediment surfaces, one crab was placed into each tray, the tray covered with 1.0 mm plastic screen, and submerged in a flowing seawater trough. Four test size classes of crabs were arbitrarily established. Each class consisted of 3 crabs of nearly identical carapace widths with class mean widths of 51.3, 64.3, 76.0, and 99.0 mm. One crab was lost from the 99.0 mm class resulting in a total of 11 crabs being tested in three 1-hour replications at 21.5° C. For each replication crabs were allowed to feed for 1 hour following a 5-minute recovery period. Individual crabs from each size class treatment were randomly assigned to a tray of clams using one-way analysis of variance (Steel and Torrie 1960). This experiment was repeated two weeks later at 25° C with another group of blue crabs having class mean widths of 25.0, 48.0, 65.7, and 91.7 mm with *M. lateralis* 3.0 to 12.2 mm in length. For each experiment crabs were starved for 24 hours prior to testing.

To observe summer mortality of *Mulinia lateralis* from causes other than predation, predator exclusion cages were utilized in the field. Plastic trays filled with sieved mud containing 10 clams were buried until their tops were level with the substrate surface. A predator exclusion cage constructed with 6.3 mm mesh plastic screen was then placed over each tray. Three pairs of exclosures were randomly arranged near ST4 and observed from mid-July to mid-September 1976.

To better interpret *Mulinia lateralis* recruitment patterns, laboratory data of Calabrese (1969b) were analyzed. Using square-root transformed counts (provided by Calabrese, personal communication), survival proportions for *M. lateralis* embryos exposed to 36 combinations of temperature (7.5, 12.5, 17.5, 22.5, 27.5, and 32.5° C) and salinity (10, 15, 20, 25, 30, and 35‰) were regressed on the full cubic in adjusted temperature and salinity. (Adjustments to temperature and salinity values were made by subtracting their medians and dividing by ($n - 1$) to prevent wide differences in scale between dependent and independent variables for the quadratic and cubic term.) Final regressions were developed using least squares analysis of the general linear model procedure in the Statistical Analysis System (SAS) (SAS Institute, Inc. 1979).

RESULTS

Habitat conditions at the five stations were very similar for most parameters (*i.e.* temperature, salinity, and phytoplankton concentration) except substrate properties and current velocity. Depths ranged from 2.0 m at ST3 to 3.5 at ST1 during high tide. Substrates differed between stations, ranging from sand at ST3 to sandy mud and silt at ST1 and ST4, but for each site, particle size composition remained relatively unchanged over time. Sediment percent organic matter varied directly with the silt-clay fraction and was highest for ST1 (3.1%) and ST4 (2.8%) and lowest at ST3 (0%) and ST5 (1.8%).

At all stations *Mulinia lateralis* abundance displayed similar seasonal periodicity between years (Fig.2). Moderate densities were persistent for several months (late winter to early summer) (Fig.2). In general, clam density was highest in late winter to early spring; declined steadily during May and June to very low summer levels; and then slowly increased again during mid-fall and early winter. Extended sampling at ST5 showed *M. lateralis* density returned to very high levels again in March 1977 (Fig. 2). Based upon preliminary sampling results showing 620 *M. lateralis* m^{-2} in March 1975, peak density in 1975 may have occurred before biweekly sampling began. Although periodicity was similar at all stations, relative abundance differed. Highest density at ST5 in 1976 was observed on March 12 and was signifi-

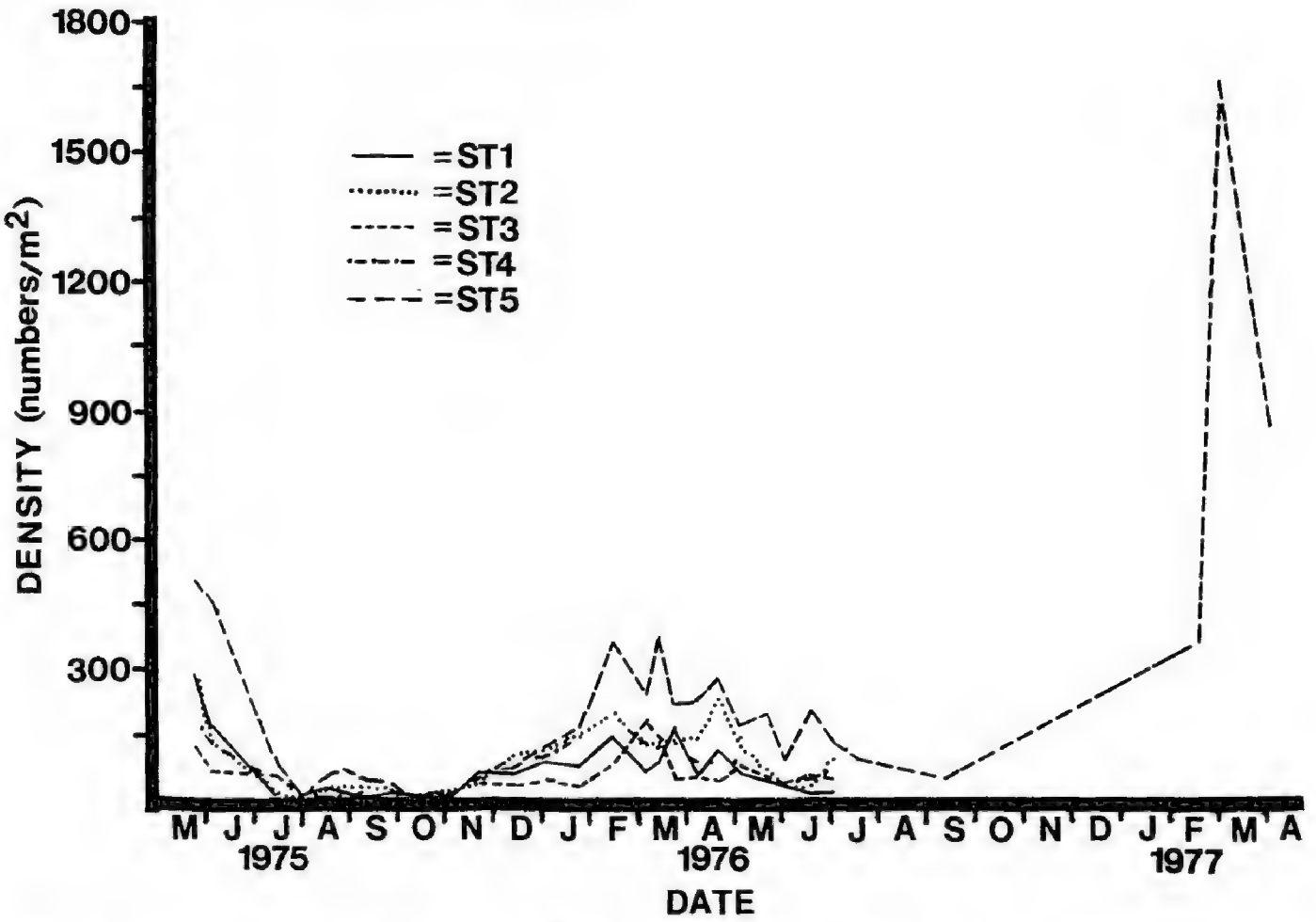

FIG. 2. Density of *Mulinia lateralis* at each sampling station (ST) for 1975–1977.

cantly greater than maximum densities at the other stations using Duncan's multiple range test (DMRT) (Steel and Torrie 1960).

Our preliminary sampling near ST5 further documented the repeatability of these *Mulinia lateralis* abundance cycles from year to year. *M. lateralis* were still relatively numerous in late June and early July 1974, but were greatly reduced by August and reached 0 m^{-2} in September 1974. By late January 1975, clam density had increased to 206 m^{-2} and extended into intertidal areas. In early spring 1975, *M. lateralis* density was as high as 620 m^{-2} in March and 500 m^{-2} in April.

Confidence limits for preliminary sample means (Table 1) showed *Mulinia lateralis* spatial distributions were random (χ^2 statistics not significant at $p = 0.05$ level) at all stations except ST2 where the distribution was aggregated. Originally, sample sizes large enough to estimate population means 20% with 95% confidence were desired for each station, however the required effort was prohibitive. Actual sample sizes for the five stations were smaller; resulting in only slightly reduced precision for all stations except ST2 (Table 1).

Smaller *Mulinia lateralis*, < 5.0 mm long, consistently predominated the samples at all stations. Larger clams were usually observed only during late spring and summer. Density of recently settled *M. lateralis* large enough to be retained in the sieve (> 1.0 mm) decreased during spring to nearly zero levels in summer 1975 (Fig. 3). Their abundance increased sharply in November 1975 and continued to rise during winter 1976 until dropping off again during

TABLE 1.

Mean ($\bar{x}$) and variance (s^2) statistics from preliminary sampling used to compute sample sizes necessary to estimate population means 20%. Actual sample sizes and associated confidence limits are also listed for each station (ST). C(ns = not significant, ** = significant at $p = 0.01$ level)

ST	Preliminary Sample Size	$\bar{x}$ (clams/grab)	s^2	2	Required Sample Size[a]	Actual Sample Size	Actual Confidence[b] Limits
1	8	15.25	26.50	12.2 ns	10	8	± 21%
2	8	15.13	45.55	21.1 **	28	5	± 47%
3	5	6.80	8.70	5.1 ns	29	17	± 26%
4	8	11.25	10.79	6.7 ns	13	6	± 29%
5	8	28.25	57.36	14.2 ns	5	3	± 26%

[a] sample size necessary to estimate population mean ± 20% with 95% confidence

[b] for a 95% confidence interval

spring 1976 (Fig. 3). A very large pulse of recruitment was also observed in February and March 1977 (Fig. 2).

Seasonal abundance changes were also observed for some *Mulinia lateralis* predators. Concurrent sampling by other researchers in the study area with a 4.5 m wide otter trawl found that fish species preying upon this clam (*i.e.* croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*) were most abundant at these shallow sites from early spring to early summer (Birkhead *et al.* 1979, Huish and Geaghan 1979). Birkhead, Bennet, Pendleton and Copeland (1977) also found that *L. xanthurus* and *M. undulatus* in nearby Dutchman Creek displayed a similar seasonal pattern. *Callinectes sapidus* seasonality was less distinct with some blue crabs being present during all seasons (Birkhead *et al.* 1979, Schwartz 1979). However, Schwartz (1979) did observe a trend towards greater crab abundance over these bottom areas in trawl samples from mid-spring through fall for 1975 and 1977 and from late winter through early summer in 1976.

In general, most predatory fish and crab species were present in the study area by early spring (Birkhead *et al.* 1979, Huish and Geaghan 1979). Our intensive trawl sampling at each benthic station from mid-March through June 1976 confirmed this observation and did not detect additional increases in predator abundance during spring. Results from the predator exclosures were inconclusive. The exclosures slowed current speeds, producing heavy sedimentation. All clams apparently died from sediment related factors based upon the numerous shells buried intact.

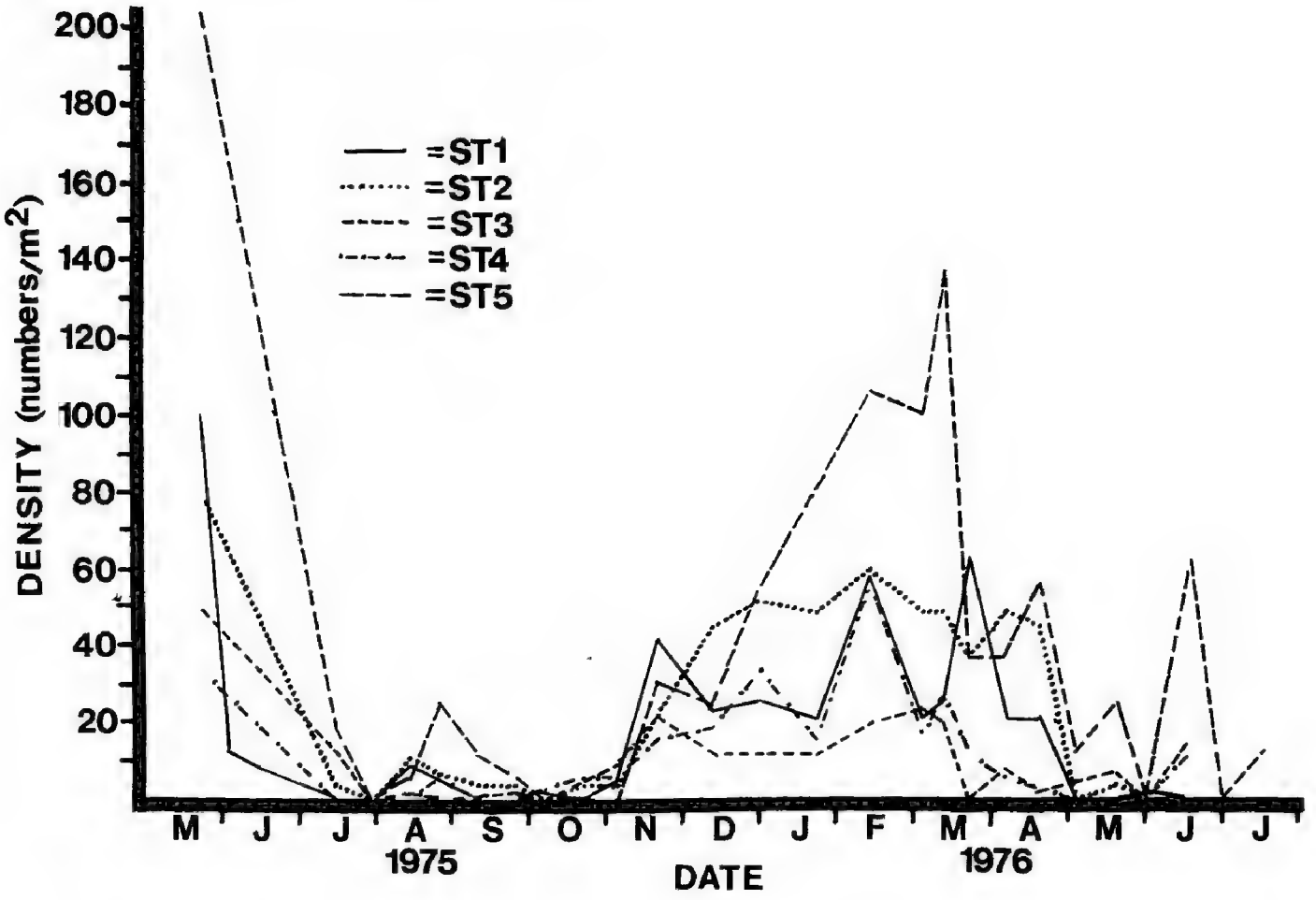

FIG. 3. Density of young *Mulinia lateralis* (≤ 2.0 mm) at each sampling station (ST) for 1975–1976.

Analysis of stomach contents from *Leiostomus xanthurus* and *Micropogonias undulatus* revealed that *Mulinia lateralis* had been consumed by both fish species. Mean length of *L. xanthurus* in our trawl samples ranged from 50 to 99 mm, while their *M. lateralis* prey ranged from < 1.0 to 3.0 mm in length. *M. undulatus* were from 53 to 121 mm long and had consumed *M. lateralis* 1.0 to 4.7 mm long. As many as seven *M. lateralis* were found in a single *L. xanthurus* stomach, while 14 *M. lateralis* were found in one *M. undulatus*. Blue crab stomachs were not inspected. Bivalve shells are generally not consumed by blue crabs (Blundon and Kennedy 1982b).

For the *Mulinia lateralis* lengths used in the feeding rate experiments, *Callinectes sapidus* were not selective in their consumption of prey sizes. No significant differences in the minimum and maximum clam lengths eaten were found between the different blue crab sizes. Feeding rates among all blue crabs ranged from 0 clams h^{-1} to 10 clams h^{-1} Rates for the largest crab size class (1.5 clams h^{-1}) were probably underestimates due to restricted crab motility in these enclosures. No significant differences were found between the overall means for experimental replications conducted at 21.5°C and at 25°C. *C. sapidus* consumed 3.2 clams h^{-1} on the average for the two experiments combined.

The regression relating *Mulinia lateralis* embryo survival data of Calabrese (1969b) to temperature and salinity was highly significant (Table 2) with an r^2

TABLE 2.

Multiple regression statistics for percentage survival of *Mulinia lateralis* embryos regressed on adjusted temperature (T) ° C and salinity (S)‰ [T = (temperature − 20)/5 and S = (salinity − 22.5)/5]. Data from Calabrese, personal communication.
(b = partial regression coefficient, r^2 = coefficient of determination, ** = significant at p = 0.0001 level

Dependent Variable	Y Intercept	Independent Variable	b	Student's t	Final r^2
% Embryo Survival	79.294				0.89 **
		T	8.950	4.51	
		S	25.477	6.49	
		TS	1.019	1.35	
		T^2	-7.245	-8.21	
		S^2	-6.371	-7.22	
		S^3	-2.046	-3.05	
		T^2S	-2.207	-4.27	
		TS^2	-1.157	-2.24	

of 0.89. Highest embryo survival was predicted between October and November and between April and June, however high values were also predicted for summer months (Fig. 4).

DISCUSSION

Population dynamics of *Mulinia lateralis* in the Cape Fear River estuary differed from abundance patterns described for this species in Long Island Sound (Sanders 1956, Levinton 1970, Levinton and Bambach 1970). Our preliminary samples and intensive biweekly sampling indicated *M. lateralis* in this more southern estuary displayed seasonally periodic changes in density repeated from summer 1974 to spring 1977. This same pattern was observed at five separate sites with different habitat conditions (Fig. 2). Similar winter to summer declines for *M. lateralis* have been reported in Chesapeake Bay (Virnstein 1977, Holland *et al.* 1980, Blundon and Kennedy 1982a) and Tampa Bay (Santos and Simon 1980). In Long Island Sound Levinton (1970) (reviewing sampling by Sanders (1956) and others) reported *M. lateralis* to be an extremely transient member of the benthos which

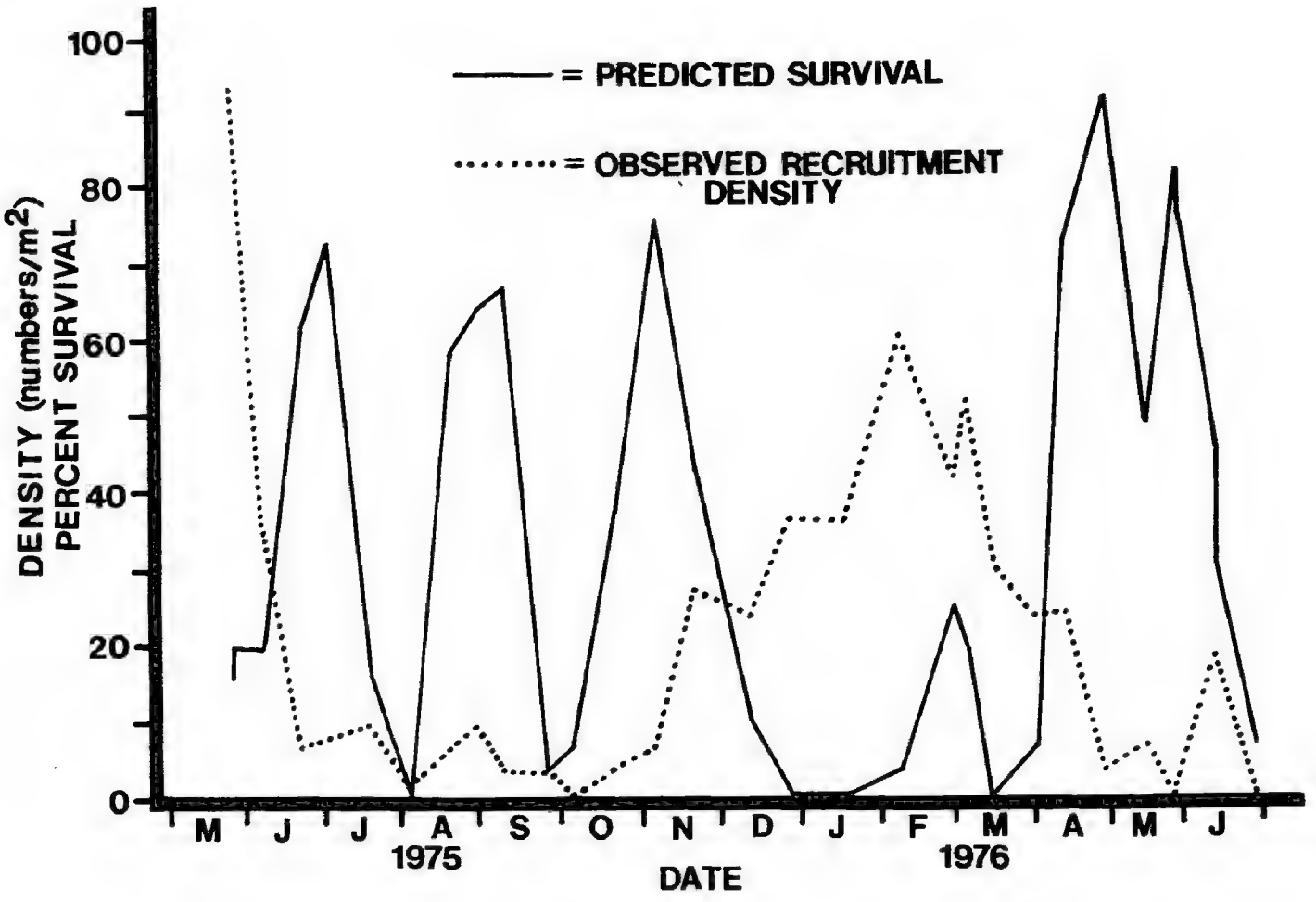

FIG. 4. A comparison of density of young *Mulinia lateralis* (≤ 2.0 mm) and predicted % survival of embryos (from the regression in Table 2.) averaged for all stations for 1975–1976.

exhibited sporadic invasions (unlike the repeated seasonality of Cape Fear River clam populations). *M. lateralis* dynamics in our study further differed from Long Island Sound populations (Levinton 1970) by displaying persistent abundance during winter and spring (Fig. 2). However, over an entire year these densities were unstable, a characteristic also described for Long Island Sound (Levinton 1970). Differences and similarities between our southern *M. lateralis* populations and those in more northern latitudes (*e.g.* Long Island Sound) must be analyzed by considering the interaction between this species' *r*-selected life history traits and its surrounding ecosystem. Our discussion will address those factors controlling reproduction and recruitment events as well as adult mortality.

The strong seasonality of *Mulinia lateralis* density appeared to be mainly a function of its reproductive cycle and changes in predator abundance and activity. Fish, *i.e. Leiostomus xanthurus* and *Micropogonias undulatus*, and blue crab predators were found to be most abundant in the study area from early spring to fall (Huish and Geaghan 1979, Schwartz 1979) and their feeding activity would increase with rising temperature. *M. lateralis* reproduction is also strongly temperature dependent and although gametogenesis occurs throughout the year, larvae were found to first appear in Long Island Sound at 16.0° C (Calabrese 1970). Based upon these findings (Calabrese 1970), temperatures in the Cape Fear River estuary were suitable for spawn-

ing during all months except December to mid-February. Changes in the seasonal coupling of recruitment and predation enabled *M. lateralis* populations to become replenished during late fall to early spring (Fig. 2).

Based upon our analyses of stomach contents and feeding rate experiments, fish and blue crabs were found to prey effectively upon *Mulinia lateralis*. Spring declines of *M. lateralis* in Chesapeake Bay were also attributed to predation by *Callinectes sapidus* and *Leiostomus xanthurus* based upon predator exclusion studies (Virnstein 1977, Holland *et al.* 1980). In our Cape Fear River study area predator seasonality (Birkhead *et al.* 1979, Schwartz 1979, Huish and Geaghan 1979) was similar to patterns in Chesapeake Bay (Miller, Sulkin and Lippson 1975, Holland *et al.* 1980) and North Carolina Sounds (Kjelson, Johnson, Garner and Bell 1974, Hester 1975) with fish and crabs being more abundant during spring and summer.

Results of our feeding-rate experiments indicated that *Callinectes sapidus* could account for appreciable mortality of *Mulinia lateralis*. Hypothetically, a minimal density of two *C. sapidus* 100 m^{-2} consuming 3.2 clams h^{-1} for 20 hours d^{-1} (feeding rates were not significantly different between night and day) could reduce *M. lateralis* density in two weeks by about 18 clams m^{-2} (excluding recruitment). Maximum observed mortality rates (excluding potential recruitment) for biweekly intervals during spring 1976 ranged from 25 clams m^{-2} at ST3 to 112 clams m^{-2} at ST5. Higher crab densities and the additional predation by spot, croaker, and other fish could account for differences between these maximal mortality rates and the minimum rates hypothesized. By comparison the horseshoe crab *Limulus polyphemus* was experimentally found to consume up to 82 *M. lateralis* d^{-1} (Botton 1984).

Other studies (Rhoads and Young 1970, Levinton 1970, Bloom *et al.* 1972, Boesch *et al.* 1976a, Santos and Simon 1980, Shumway 1983) proposed that stressful environmental conditions of substrate, temperature, salinity, dissolved oxygen, or other abiotic factors could account for high *Mulinia lateralis* mortalities and population declines. In the Cape Fear River, predation seemed more important. None of these environmental conditions in the Cape Fear River varied in a manner consistent with spring *M. lateralis* declines to very low summer densities. Temperature remained below an upper tolerance limit of 33.5° C reported for *M. lateralis* (Kennedy and Mihursky 1971) and salinity varied irregularly during spring (generally > 15‰). Dissolved oxygen levels were also adequate for survival generally remaining above 4.0 ppm throughout spring and 2.8 ppm in summer (Birkhead *et al.* 1979). Even during short-term periods of anoxia, this clam can maintain high levels of feeding and activity (Shumway, Scott and Shick 1983). Shumway and Newell (1984) hypothesized that stressful effects of high temperature, low dissolved oxygen, and low food could account for the sharp density declines frequently observed for *M. lateralis*. Dynamics of Cape Fear River *M. lateralis* were not consistent with this hypothesis. Low summer densities did not occur catastrophically, but followed a steady spring decline. Habitat physical conditions may be a more significant source of *M. lateralis* mortality in some other systems, *e.g.* substrate instability in Long Island

Sound (Levinton 1970) or hypoxia in portions of Tampa Bay (Santos and Simon 1980).

Turbidity with potential filter clogging has been suggested as a mortality factor for *Mulinia lateralis* and other bivalves in muddy substrates (Jackson 1968, Rhoads and Young 1970, Bloom *et al.* 1972, Levinton 1970, Boesch *et al.* 1976a). In our study area susceptible, newly recruited clams could have experienced high mortality (not detected by our methods) due to flocculent sediments. Luckenbach (1984) observed differential survival of newly settled *M. lateralis* in South Carolina intertidal communities which may have been due to sediment instability. The relative effects of physically-induced mortality *versus* predation are probably partitioned between clam size classes. Substrate effects did not appear to control the steady spring declines of larger *M. lateralis* in the Cape Fear River. Grain size composition did not change significantly over time at each site and although stations differed widely in silt-clay and organic content, they exhibited similar seasonality in adult clam density. Seasonal mortality of clams > 1.0 mm in our study and in Chesapeake Bay (Virnstein 1977, Holland *et al.* 1980, Blundon and Kennedy 1982a) was greatly dependent upon predation.

As an *r*-strategist, *Mulinia lateralis* exhibits a high fecundity [up to 7×10^6 eggs per female (Calabrese 1969a)], enabling population densities to potentially recover quickly from high mortality events. In Long Island Sound, this adaptation apparently allowed *M. lateralis* to opportunistically colonize vacant bottom areas following reductions in interspecific competition (Levinton and Bambach 1970). However, sediment regimes in Long Island Sound were such that heavy juvenile clam mortality occurred, quickly depleting these *M. lateralis* invasions (Levinton and Bambach 1970). In the Cape Fear River, an important nursery area for spot, croaker, and blue crabs (Birkhead *et al.* 1979), this high fecundity counteracted the seasonal effects of predation. Multiple spawning intervals could also ameliorate the loss of newly settled clams due to random events of substrate disturbance.

Warmer climatic conditions in our study area (extending the spawning season for *Mulinia lateralis*) could help account for the geographical differences in population dynamics mentioned previously. Based upon *M. lateralis* reproductive studies of Calabrese (1970), it was determined that Cape Fear River temperatures were suitable for spawning during most of the year except winter. Similarly, observed recruitment of small clams, 1.0 to 2.0 mm (Fig. 3), occurred throughout all seasons although it was greatest during late fall through early spring. In Chesapeake Bay, Blundon and Kennedy (1982a) similarly found newly settled *M. lateralis* throughout most of the year. A number of variables including phytoplankton abundance and composition, temperature, salinity, predation, and circulation patterns determine the proportion of larvae eventually reaching the benthos. However, an extended spawning season would increase the probability of clam population recoveries from seasonal predation or turbidity events, producing less transient abundance patterns. With an average generation time of 60 days (Calabrese

1969a) this extended spawning season would also allow multiple generation spawning.

A comparison of seasonal recruitment of young clams to predicted embryo survival (Fig. 4) helped define the adaptive significance of *Mulinia lateralis* *r*-selected reproduction in the Cape Fear River estuary. Potential spawning patterns during the extended reproductive season for *M. lateralis* can be inferred by using larval data of Rhodes, Calabrese, Cable and Landers (1972) and Calabrese (1969a,b). It must be noted, however, that estuarine circulation, water quality, and planktonic predation can greatly modify the relationship between predicted embryo survival (theoretical spawning success based on temperature and salinity effects only) and observed clam recruitment (Fig. 4). In spite of these limitations, survival regression predictions should still indicate which months could be physiologically more important to *M. lateralis* reproduction, especially due to the important role of temperature in bivalve spawning (Bayne 1976) and larval survival (Calabrese 1969b). Higher predicted embryo survival occurred during all months except winter (Fig. 4), similar in duration to the extended spawning season discussed above. Increasing density of young clams during winter 1976 probably resulted from clams slowly growing to a catchable size after being spawned and settling during fall (Fig. 4). Future studies could directly test these theoretical spawning and recruitment patterns using methods similar to Luckenbach (1984).

Seasonal predation apparently masked the actual magnitude of *Mulinia lateralis* reproduction and recruitment during late spring and summer (Fig. 3). Benthic predation (*e.g.* by fish and crabs), as well as planktonic and meiofaunal predators (Thorson 1966), and abiotic factors (Luckenbach 1984) could have contributed strongly to the paucity of young clams observed during warmer months (Fig. 3). Additionally, the pattern of clam recruitment increasing from fall to early spring (Fig. 4) coincided with reduced predator abundance and activity. Virnstein (1977) and Holland *et al.* (1980) reported that *M. lateralis* and other bivalves settling to the benthos during summer were rapidly cropped by predation.

The role of predation in masking the actual magnitude of *Mulinia lateralis* recruitment during spring to summer was directly observed at ST5 during June 1976. Small *M. lateralis* ($\leq$ 2.0 mm) increased sharply in density (Fig. 3) during mid-June. However, two weeks later, density of these recruits was greatly reduced, while *M. lateralis* in stomach contents of *Leiostomus xanthurus* from ST5 increased sharply. These spot apparently took advantage of an exceptionally strong *M. lateralis* recruitment pulse, large enough to be detected by sampling despite high cropping rates. Dead-shell frequencies could not be used to evaluate the additional contribution of abiotic factors to this mortality event in the Cape Fear River as had been done in Long Island Sound by Levinton and Bambach (1970). Observations of blue crabs feeding on *M. lateralis* revealed that at least one valve was frequently left undamaged, confounding the interpretation of Cape Fear River dead-shell assemblages.

Our previous discussion of biogeographic differences between the dynamics of southeastern *Mulinia lateralis* and those in more northern habitats, *e.g.* Long Island Sound, emphasized climatic factors and predator seasonality. The repeated seasonal periodicity observed for *M. lateralis* in the Cape Fear River (Fig. 2) may be representative of populations in other southern estuaries. A simultaneous comparison of *M. lateralis* abundance changes for estuaries ranging from Chesapeake Bay (Boesch 1973, Boesch *et al.* 1976a, Holland *et al.* 1980) to North Carolina (Tenore 1970; Price, Thayer and Montgomery 1974) and South Carolina (Stickney and Perlmutter 1975) revealed a general seasonality (Fig. 5) similar to Cape Fear River populations (Fig. 2). The failure of "YEAR 3" data of Boesch *et al.* (1976a) to show a winter-spring peak (Fig. 5) might be explained if highest numbers occurred between the quarterly sampling dates.

Our findings stress the need for frequent sampling (at least biweekly) of dynamic species such as *Mulinia lateralis*. Due to an extended spawning season with rapid growth and maturity, longer sampling intervals would underestimate the contribution of this clam to benthic food webs and miss shorter-lived pulses of recruitment. Most previous studies used quarterly sampling intervals (Tenore 1970, Boesch 1973, Price *et al.* 1974, Boesch *et al.* 1976a). Differences between *M. lateralis* population dynamics in southern

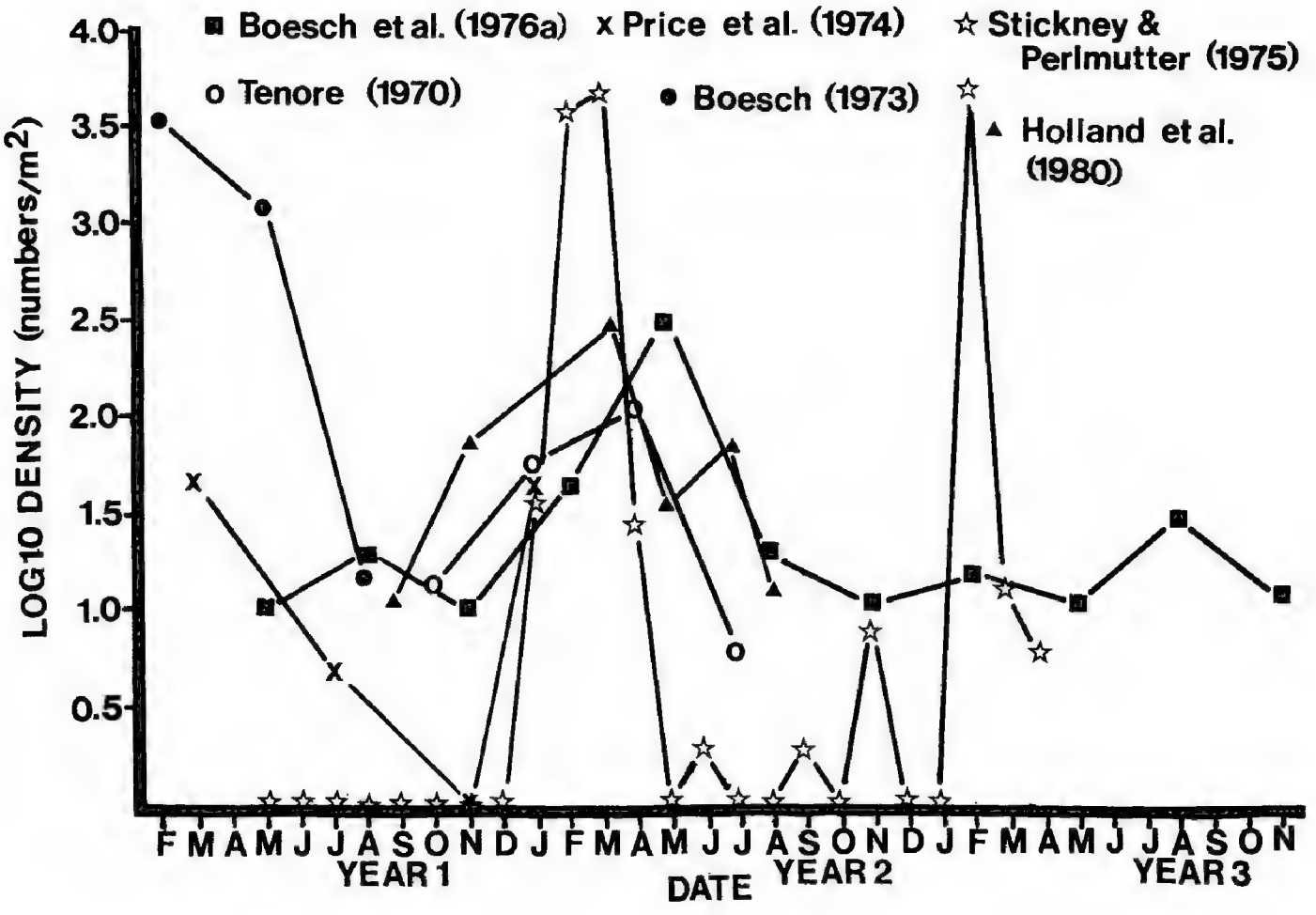

FIG. 5. Comparisons of *Mulinia lateralis* density seasonality from previous studies. Data from the first year of a particular study are plotted beginning in YEAR 1.

estuaries compared to Long Island Sound should reflect the relative importance of this clam geographically to benthic food webs.

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LITERATURE CITED

BAYNE, B.L. 1976. Aspects of reproduction in bivalve molluscs. pp. 432–448. In M.L. Wiley (ed.) *Estuarine Processes,* Vol. 1. Academic Press, N.Y.

BIRKHEAD, W.S., C.R. BENNET, E.C. PENDLETON and B.J. COPELAND. 1977. Nursery utilization of the Dutchman Creek estuary, N.C., 1971–1976. North Carolina State University Report No. 77-2 to Carolina Power and Light Co., Raleigh, N.C. 258 p.

BIRKHEAD, W.A., B.J. COPELAND and R.G. HODSON. 1979. Ecological monitoring in the lower Cape Fear River estuary 1971–1976. North Carolina State University Report No. 79-1 to Carolina Power and Light Co., Raleigh, N.C. 292 p.

BLOOM, S.A., J.L. SIMON and V.D. HUNTER. 1972. Animal-sediment relations and community analysis of a Florida estuary. *Marine Biology.* 13:43–56.

BLUNDON, J.A. and V.S. KENNEDY. 1982a. Refuges for infaunal bivalves from blue crab *Callinectes sapidus* predation in Chesapeake Bay USA. *Journal of Experimental Marine Biology and Ecology.* 65:67–82.

_____ and _____. 1982b. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *Journal of Experimental Marine Biology and Ecology.* 65:47–65.

BOESCH, D.F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology.* 21:226–244.

_____, R.J. DIAZ and R.W. VIRNSTEIN. 1976a. Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesapeake Science.* 17:246–259.

_____, M.L. WASS and R.W. VIRNSTEIN. 1976b. The dynamics of estuarine benthic communities. pp. 177–196. In M.L. Wiley (ed.) *Estuarine Processes,* Vol. 1. Academic Press, N.Y.

BOTTON, M.L. 1984. Diet and food preferences of the adult horseshoe crab *Limulus polyphemus* in Delaware Bay, New Jersey, USA. *Marine Biology.* 81:199–207.

BREUER, J.P. 1957. An ecological survey of Baffin and Alazan Bays, Texas. *Publications of the Institute of Marine Science, University of Texas.* 4:134–155.

BUCHANAN, J.B. and J.M. KAIN. 1971. Measurement of the physical and chemical environment. pp. 30–58. In N.A. Holme and A.D. McIntyre (eds.) *Methods for the Study of Marine Benthos.* Blackwell Scientific Publication, Oxford.

CALABRESE, A. 1969a. *Mulinia lateralis:* molluscan fruit fly? *Proceedings of the National Shellfish Association.* 59:65–66.

_____. 1969b. Individual and combined effects of salinity and temperature on embryos and larvae of the coot clam, *Mulinia lateralis* (Say). *Biological Bulletin.*137:417–428.

_____. 1970. Reproductive cycle of the coot clam, *Mulinia lateralis* (Say), in Long Island Sound. *The Veliger.* 122:265–269.

DENT, S.R. 1983. The effects of the hermit crab *Clibanarius vittatus* (Bosc 1802) on the structure of a shallow bay macroinfaunal community. M.S. Thesis. Texas A&M University, College Station. 167 p.

ELLIOTT, J.M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association Scientific Publication.* No. 25. Westmorland, England 148 p.

FOLK, R.L. 1968. *Petrology of Sedimentary Rocks.* Hemphill's, Austin,Texas 170 p.

HESTER, J.M. 1975. Nekton population dynamics in the Albemarle Sound and Neuse River estuaries. University of North Carolina Sea Grant Publication UNC-SG-75-02. Raleigh, N.C. 129 p.

HOBBIE, J.E. 1971. Some ecological measurements of the Cape Fear River, N.C. North Carolina State University Report to Carolina Power and Light Co. Raleigh, N.C. 107 p.

HOLLAND, A.F., N.K. MOUNTFORD, M.H. HIEGEL, K.R. KAUMEYER and J.A. MIHURSKY. 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. *Marine Biology.* 57:221–235.

HUISH, M.T. and J.P. GEAGHAN. 1979. A study of adult and juvenile fishes of the lower Cape Fear River near the Brunswick steam electric plant 1975–1976. North Carolina State University Report No. 79-4 to Carolina Power & Light Co. Raleigh, N.C. 148 p.

JACKSON, J.B.C. 1968. Bivalves: spatial and size-frequency distribution of two intertidal species. *Science.* **161**:479–480.

KENNEDY, V.S. and J.A. MIHURSKY. 1971. Upper temperature tolerances of some estuarine bivalves. *Chesapeake Science.* **12**:193–204.

KJELSON, M.A., G.N. JOHNSON, R.L. GARNER and R. BELL. 1974. Estimated biomass for nekton communities and populations in the Newport River estuary and an evaluation of nekton sampling methods. pp. 207–237. In National Marine Fisheries Service Southeast Fisheries Center Annual Report to Atomic Energy Commission for 1974. National Marine Fisheries Service Laboratory, Beaufort, N.C.

LEATHEM, W., P. KINNER, D. MAURER, R. BIGGS and W. TREASURE. 1973. Effect of spoil disposal on benthic invertebrates. *Marine Pollution Bulletin.* **4**:122–125.

LEVINTON, J.S. 1970. The paleoecological significance of opportunistic species. *Lethaia.* 3:69–78.

_____ and R.K. BAMBACH. 1970. Some ecological aspects of bivalve mortality patterns. *American Journal of Science.* **268**:97–112.

LUCKENBACH, M.W. 1984. Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia). *Marine Ecology — Progress Series.* **17**:245–250.

MILLER, R.E., S.D. SULKIN and R.L. LIPPSON. 1975. Composition and seasonal abundance of the blue crab, *Callinectes sapidus* (Rathbun), in the Chesapeake and Delaware Canal and adjacent waters. *Chesapeake Science.* **16**:27–31.

PARKER, R.H. 1975. *The Study of Benthic Communities: a Model and a Review.* Elsevier Scientific Publishing Co., N.Y. 279 p.

PRICE, T.J., G.W. THAYER and G.B. MONTGOMERY. 1974. Analysis of the invertebrates and sediments along shore to shore transects in the Newport River estuary. pp. 183–198. In National Marine Fisheries Service Southeast Fisheries Center Annual Report to Atomic Energy Commission for 1974. National Marine Fisheries Service Laboratory, Beaufort, N.C.

RHOADS, D.C. and D.K. YOUNG. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research.* **28**:150–178.

RHODES, E.W., A. CALABRESE, W.D. CABLE and W.S. LANDERS. 1972. The development of methods for rearing the coot clam, *Mulinia lateralis*, and three species of coastal bivalves in the laboratory. pp. 273–282. In W.L. Smith and M. H. Chanley (eds.) *Culture of Marine Invertebrate Animals*, Plenum Publishing Co., N.Y.

SANDERS, H.L. 1956. Oceanography of Long Island Sound, 1952–54. X. The biology of marine bottom communities. *Bulletin of the Bingham Oceanographic Collection.* **15**:345–414.

SANTOS, S.L. and J.L. SIMON. 1980. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. *Marine Ecology — Progress Series.* 3:347–355.

SAS INSTITUTE, INC. 1979. *SAS User's Guide, 1979 Edition.* SAS Institute, Inc. Raleigh, N.C. 494 p.

SCHWARTZ, F.J. 1979. An ecological study of fishes and invertebrate macrofauna utilizing the Cape Fear River estuary, Carolina Beach inlet, and adjacent Atlantic Ocean. University of North Carolina Annual Report for 1976, Vol. XIVd to Carolina Power and Light Co. Raleigh, N.C. 293 p.

SHUMWAY, S.E. 1983. Factors affecting oxygen consumption in the coot clam *Mulinia lateralis* (Say). *Ophelia.* 22:143–171.

_____ and R.C. NEWELL. 1984. Energy resource allocation in *Mulinia lateralis* (Say), an opportunistic bivalve from shallow water sediments. *Ophelia.* 23:101–118.

_____, T.M. SCOTT and J.M. SHICK. 1983. The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, *Mulinia lateralis* (Say). *Journal of Experimental Marine Biology and Ecology.* 71:135–146.

STEEL, R.G.D. and J.H. TORRIE. 1960. *Principles and Procedures of Statistics.* McGraw-Hill, N.Y. 481 p.

STICKNEY, R.R. and D. PERLMUTTER. 1975. Impact of intracoastal waterway maintenance dredging on a mud bottom benthos community. *Biological Conservation.* 7:211–226.

TAGATZ, M.E. 1968. Biology of the blue crab, *Callinectes sapidus* (Rathbun), in the St. John's River, Florida. *Fishery Bulletin.* 67:17–23.

TENORE, K.R. 1970. The Macrobenthos of the Pamlico River Estuary, N.C. Ph.D. Dissertation. North Carolina State University, Raleigh, N.C. 121 p.

THORSON, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands Journal of Sea Research.* 3:267–293.

VIRNSTEIN, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology.* 58:1199–1217.

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MOVEMENT, GROWTH AND SURVIVAL OF SPOTTED SEATROUT TAGGED IN BASTROP BAYOU, TEXAS

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ABSTRACT

During February 1976–November 1981, 2040 spotted seatrout (*Cynoscion nebulosus*) were caught for tagging with hook and line at Bastrop Marina on Bastrop Bayou in the Galveston Bay system.

The subsequent tag return rate was 8.6% (176 individuals). Tag recapture data indicate an exit of fish from the Bayou in winter months with a return in the spring, followed by a summer exit and a subsequent fall return. Along with this cyclical pattern, a possible migratory behavior pattern emerged when virtually no recaptures appeared in adjacent tributaries even though spotted seatrout are frequently harvested in these adjacent areas. This suggests the possibility of sub-populations within Galveston Bay. Forward stepwise regression analyses indicate that total length at release, number of warm days free and number of cold days free accounted for 60.28% of the variation in total length at recapture. Survival of spotted seatrout tagged in fall ranged from 20–33% per year.

INTRODUCTION

Spotted seatrout (*Cynoscion nebulosus*) is an important commercial and recreational fish on both the Atlantic and Gulf coasts of the United States. Commercial U.S. landings in 1981 were 1.77 million kg (National Marine Fisheries Service 1982). Recreational landings in 1979 were 6.6 million fish (National Marine Fisheries Service 1980). In Texas spotted seatrout comprise 41% of the recreational landings; no legal commercial harvest has been allowed since 1981 (Anonymous 1983). Effective management of this fishery requires information on movement, growth and survival to identify stock boundaries and conduct yield modeling.

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Current literature on movement of spotted seatrout is inconsistent. Fish tagged in Florida moved generally ≤ 48 km without pattern (Moffett 1961; Iversen and Moffett 1962; Ingle, Hutton and Topp 1962; Iversen and Tabb 1962). Fish tagged in a Texas bay apparently moved to the Gulf in summer and returned to the same estuary in the fall (McEachron and Matlock 1980). In Georgia and Texas spotted seatrout catches in experimental nets indicated movement from shallow to deep waters within estuaries in summer and winter (Mahood 1974, Pearson 1929, Gunter 1945, Simmons 1951, Guest and Gunter 1958). Efforts in Florida using protein biosystematic analyses indicated that each major estuarine system had its own subpopulation (Weinstein 1975, Weinstein and Yerger 1976).

Growth rates of spotted seatrout have been examined using scales and tagged fish. However, few fish were involved (Pearson 1929, Moffett 1961), and the scale method has not been verified (Miles 1950; Colura, Porter and Maciorowski 1984).

Survival estimates of spotted seatrout have also received little attention. Estimates of 55.3% annual survival were derived in Florida using tagged fish (Iversen and Moffett 1962). There are no known published estimates of survival in Texas. Length frequency data from an annual spotted seatrout fishing tournament conducted in Alabama revealed an 8-year mean annual survival rate of 50.2% for III+ and older fish (Tatum 1978).

The objective of this study was to estimate growth and survival, and describe the movement of spotted seatrout tagged in Bastrop Bayou, Texas.

MATERIALS AND METHODS

Spotted seatrout were caught on hook and line at Bastrop Marina on Bastrop Bayou (Fig. 1) from February 1976 through November 1981. Before tagging fish were held for 1–7 days without supplemental food in a wood-slat crate measuring 1.2 × 1.2 × 1.2 m. Fish in apparently good condition were measured to the nearest mm total length (*TL*) (Fig. 2), then tagged with an internal abdominal tag with an external plastic yellow streamer as described by Moffett (1961). Uniquely numbered tags were made of semi-hard glossy green, blue or red plastic (25.4 × 6.4 × 0.8 mm) with round corners and "Texas PWD Seabrook" or "Texas PWD Rockport" printed on each tag.

The tagging was publicized by placing posters at sporting goods stores, boat ramps, fishing piers and commercial fish houses. Additional publicity was gained through local newspapers, radio stations and television stations. Individuals returning tags were requested to provide the species, *TL* and/or weight, date and location of catch. Rewards from $1.00 to $25.00 were paid for each tag by the National Marine Fisheries Service or the Gulf Coast Conservation Association as an incentive for tag returns.

Assumptions employed in analyses of movement data incorporated those reported by Osburn, Matlock and Green (1982):

(1) Information obtained from fishermen on returns was valid;
(2) There were no behavioral differences between tagged and untagged fish;
(3) There was approximately equal fishing pressure and/or success in all areas where fish may have moved; and
(4) Tag loss was insignificant.

If vital information concerning length at recapture, location of recapture, or date of recapture was absent, the tag return data were disregarded in the appropriate calculations.

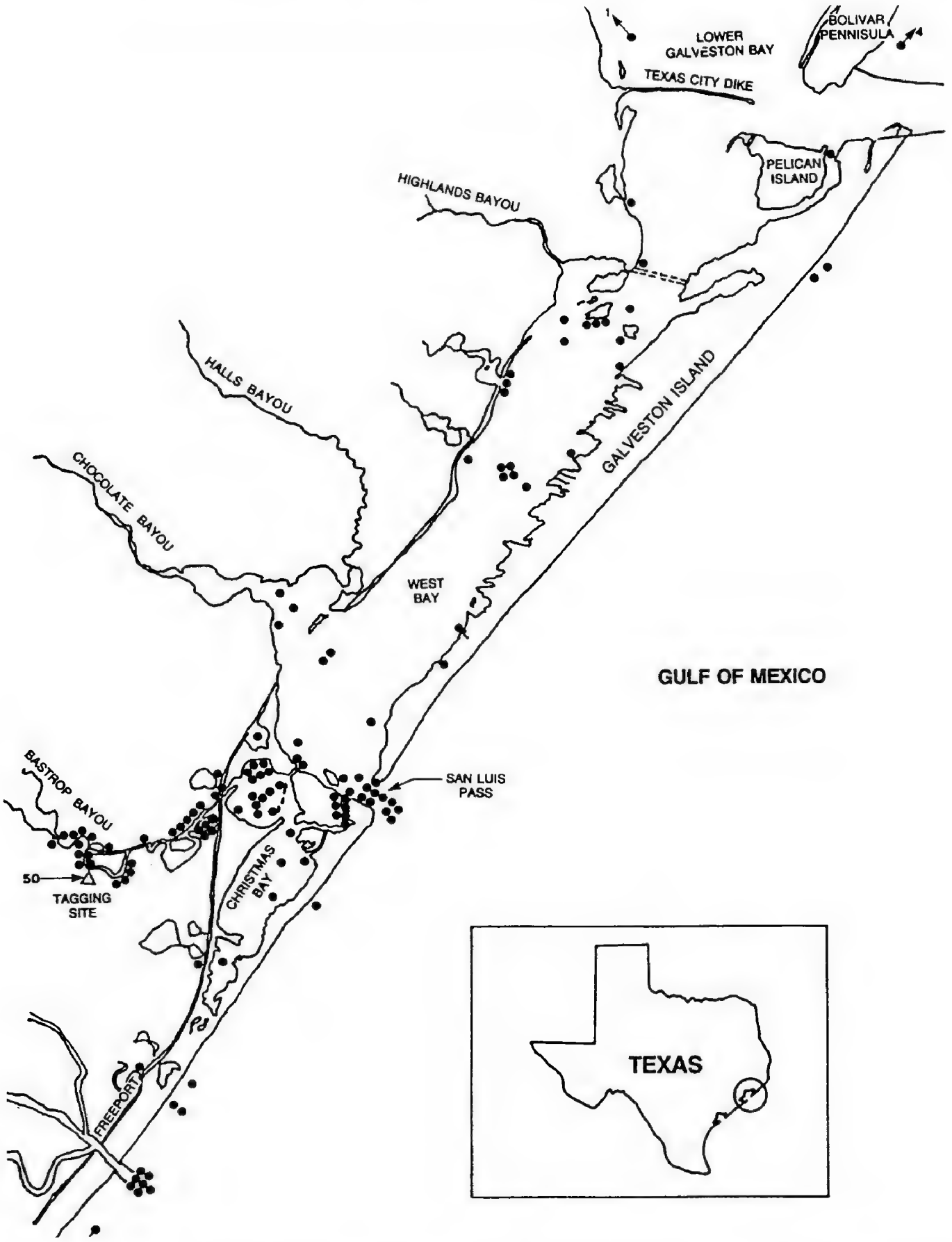

FIG. 1. Recapture sites of *Cynoscion nebulosus* tagged in Bastrop Bayou, Texas (February 1976–November 1981.)

Minimum distances traveled were determined by plotting the tagging and recapture sites and measuring the shortest aquatic distance (to the nearest km) between the two sites on appropriate NOAA Nautical Charts. The relationship between distance traveled and time free was examined separately for fish tagged in September, October, and November using linear regression (Sokal and Rohlf 1969). Each recapture date was expressed as Julian date, multiplied by 0.986 to adjust

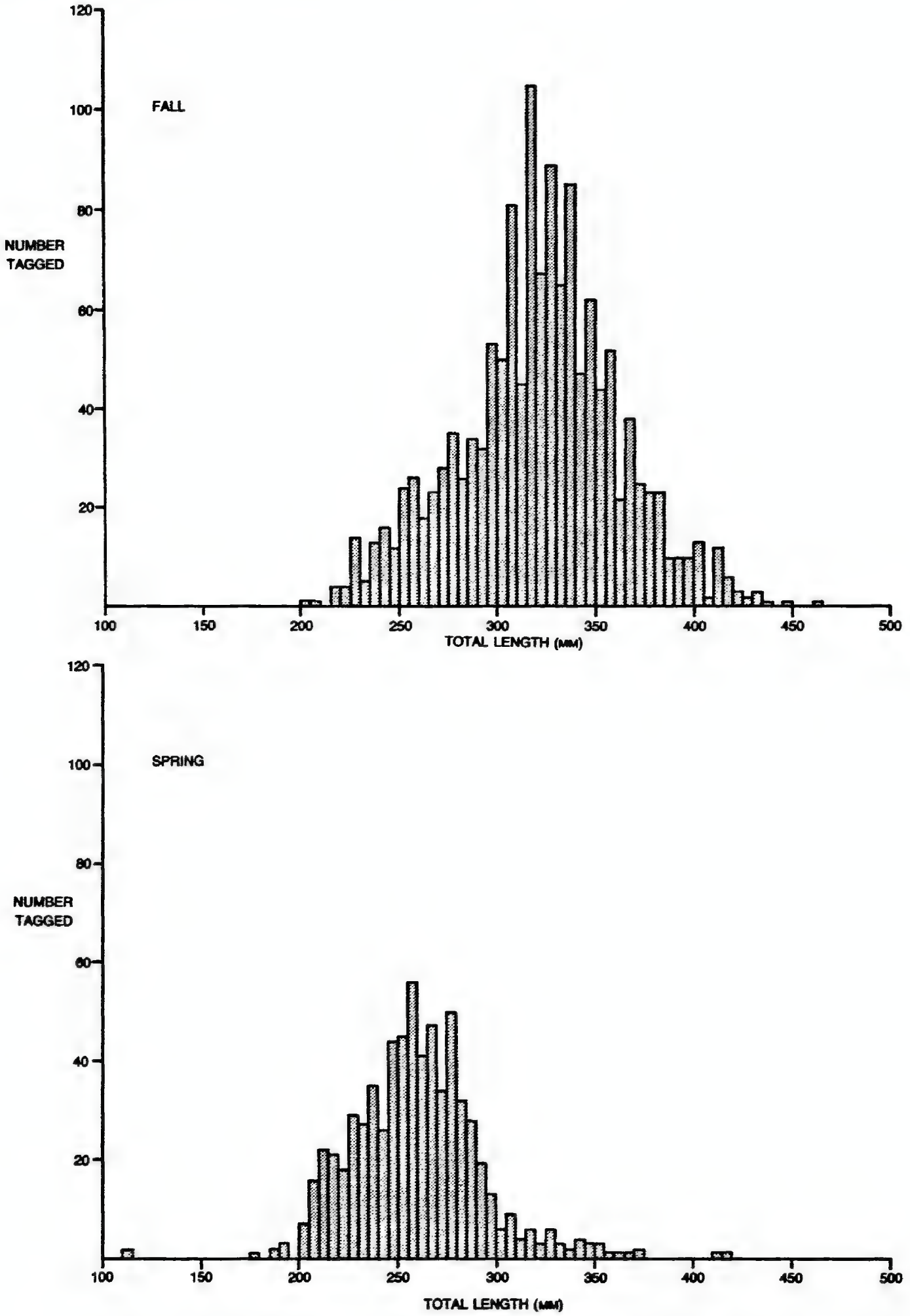

FIG. 2. Length frequency of *Cynoscion nebulosus* tagged in Bastrop Bayou, Texas during spring (February–March 1976, April 1978, March–April 1981) and fall (September–October 1976, November 1977, September–November 1980, November 1981.)

the year to 360 days, and then 106, 136, or 167 was added to adjust all release dates to the 15th of each month. The sine of each of these values was converted to the absolute value.

Growth of fish released in both fall and spring was examined using a forward stepwise regression (Draper and Smith 1966) with *TL* at recapture regressed on *TL* at release, number of warm days free (maximum air temperature ≥ 15° C), and number of cold days free. This temperature (15° C) was selected as the expected point at which growth would decline dramatically based on oxygen consumption data from Wohlschlag (1981). Days free included the tagging date but excluded the recapture date. Temperature data were obtained for Galveston, Texas from NOAA Climatological Data Monthly Weather Summaries 1976–1983.

Survival (*S*) was estimated for three groups of fish tagged in the fall following Ricker (1975, p.105). The relation

$$\mu = FA/Z \qquad \text{(Ricker 1975, page 11)}$$

was used to estimate annual instantaneous fishing mortality (*F*) where

$$\mu = \text{exploitation rate}$$

and $A = 1 - S$. Solving for F yields:

$$F = \mu Z/A.$$

Minimum exploitation rate was estimated by adjusting the number of reported tags (R_1) by the reporting rate 0.33 (Green, Matlock and Weaver 1983). Once F was estimated, the annual instantaneous natural mortality (*M*) was estimated by subtraction.

$$M = Z - F.$$

RESULTS

During February 1976–November 1981, 2040 spotted seatrout were tagged. The tag return rate was 8.6% (176 individuals).

Movement of spotted seatrout tagged in Bastrop Bayou was cyclical and almost completely restricted to the Bayou and adjacent bay areas. Returns from the nearby Gulf and pass occurred in warm months only. Tag recapture data indicated an exit of fish from the Bayou in winter months with a return in the spring, followed by a summer exit and a subsequent fall return (Fig. 3 and Table 1). There were no tag returns from other major tributaries in the surrounding area (Fig. 1). A significant relationship between distance from Bastrop Bayou and time free (Julian recapture date) was found using data for fish released in September, October, November (Table 2). However, the regression explained only 15–36% of the variation.

The growth of the seatrout depended on their size at tagging and temperature. The forward stepwise regression analyses indicatedthat total length at release (TL_R), number of warm days free (*WARM*), and the number of cold days free (*COLD*) accounted for 60.25% of the variation in total length at recapture (TL_C) (Table 3). The resultant equation was

$$TL_C = 164.592 + 0.522\,TL_R + 0.387\,WARM - 0.606\,COLD \text{ (Table 3).}$$

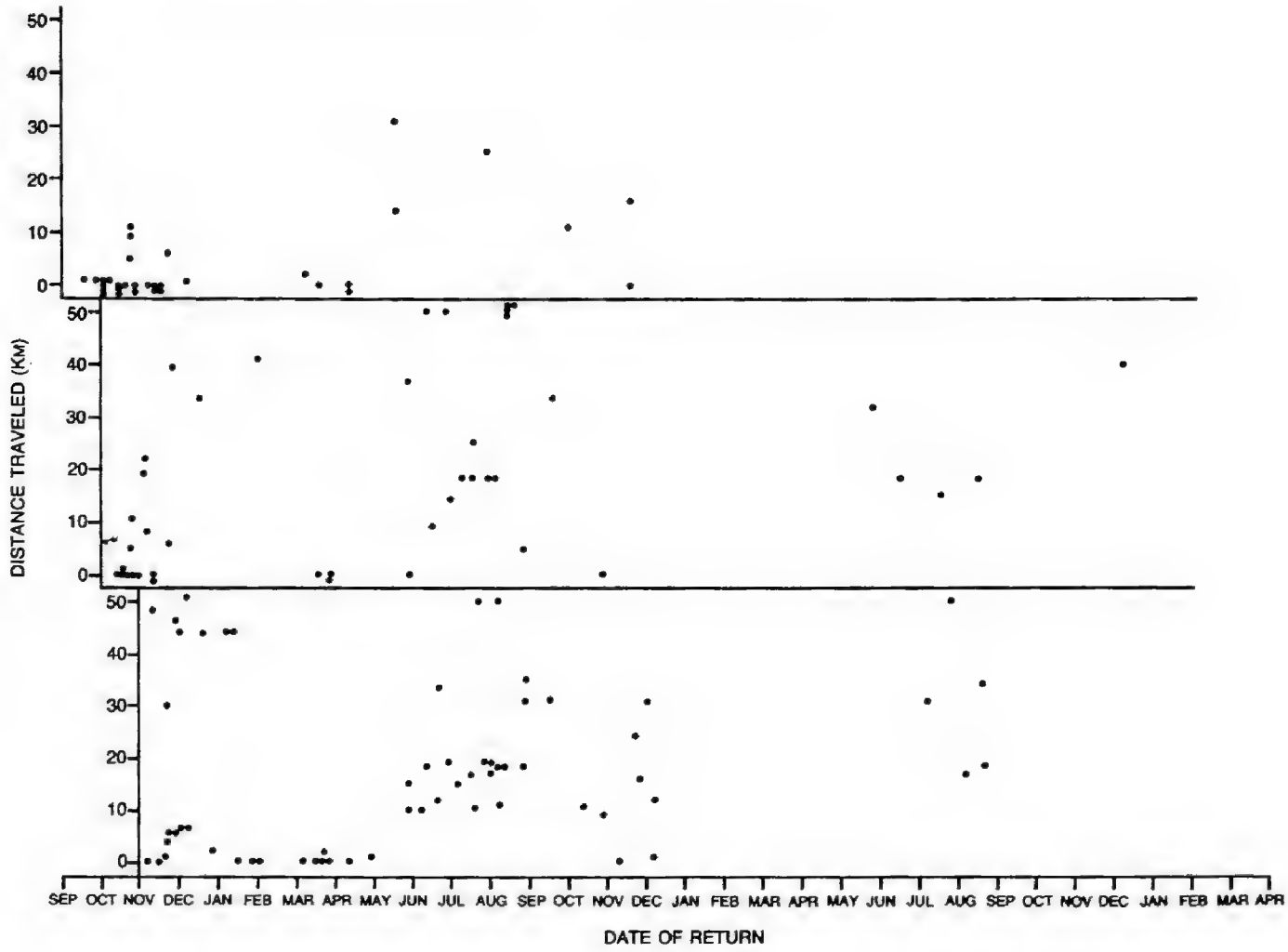
DISTANCE TRAVELED (KM)
0
10
20
30
40
50
SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR
DATE OF RETURN

FIG. 3. Minimum distance traveled by *Cynoscion nebulosus* tagged in fall at Bastrop Bayou, Texas (first month in each graph indicates month of release.)

Survival of spotted seatrout tagged in fall ranged from 20–33% per year (Table 4). Natural mortality (M) accounted for most (61–80%) of the mortality.

DISCUSSION

Subgroups of spotted seatrout populations may exist within tributaries of bays with some mixing among subgroups possibly occurring in bays and the adjacent Gulf of Mexico. This conclusion is supported by: 1) an apparent seasonal movement of trout between the riverine end of bays and the Gulf; 2) the lack of any returns from adjacent major bays (*e.g.*, Galveston and East Matagorda Bay) or adjacent tributaries within the area of tagging (*e.g.*, Chocolate, Halls and Highlands Bayous) even though recreational fishermen frequently harvest trout in these adjacent areas (TPWD unpublished data); and 3) the return of tags from the Gulf only during summer even though sport fishermen frequently fish in the Gulf all year (Springer and Pirson 1958, Trent 1976, McEachron 1980, McEachron and Green 1984). Moffett (1961) suggested the existence of sub-populations among bays but did not examine the possibility of within-bay groups. If such subgroups do exist, additional research is needed to determine the role of bay-gulf movements.

TABLE 1

Percent of *Cynoscion nebulosus* tagged in Bastrop Bayou, Texas, in fall and spring that were returned in Bastrop Bayou, bays, and in or near the Gulf of Mexico.

Fall Tagged Fish (*N*=140)

Season of return	Bastrop Bayou recaptures	Bay recaptures	Pass/Gulf recaptures	Total
Spring	11	3	2	16
Summer	1	16	14	31
Fall	30	11	0	41
Winter	6	6	0	12

Spring Tagged Fish (*N*=33)

Season of return	Bastrop Bayou recaptures	Bay recaptures	Pass/Gulf recaptures	Total
Spring	12	9	0	21
Summer	0	30	15	45
Fall	15	9	3	27
Winter	3	3	0	6

TABLE 2

Results of regression analyses of tag returns of fall tagged fish at Bastrop Bayou, Texas (September 1976–November 1981)

Fall Tagged Fish

Month	*N*	*Y*-intercept	Slope	*R*
September	34	-2.94	14.86	0.42
October	42	68.65	- 63.41	-0.60
November	61	29.02	- 21.26	-0.39

TABLE 3

Results of forward stepwise regression of total length of warm days at recapture versus total length at release (TL_R), number of warm days (*WARM*) and number of cold days (*COLD*) free for fish released in fall and spring.

Step	Y-intercept	Variable added	Coefficient ± 1 SE	R^2	F (degrees of freedom)
0	379.845				
1	317.771	*WARM*	0.330 ± 0.035	0.515	90.14** (1,85)
2	199.338	TL_R	0.388 ± 0.116	0.571	55.97** (2,84)
3	164.592	*COLD*	-0.606 ± 0.236	0.603	31.99** (3,83)
Summary	164.592	TL_R	0.522 ± 0.124		
		WARM	0.387 ± 0.048		
		COLD	-0.606 ± 0.236	0.603	41.99** (3,83)

** $P < .01$

TABLE 4

Estimates of exploitation rate (μ) adjusted for a nonreporting rate of 0.67 (Green *et al.* 1983), annual instantaneous rates of total (Z), fishing (F), and natural (M) mortalities for three groups of *Cynoscion nebulosus* tagged in Bastrop Bayou, Texas.

Release period	Number tagged	Number recaptured Year 1	Number recaptured Year 2	μ	S	Z	F	M
Sep-Oct 1976	398	24	5	0.18	0.21	1.57	0.36	1.21
Sep-Oct 1980	428	20	4	0.14	0.20	1.61	0.28	1.33
Nov 1980	363	28	9	0.23	0.32	1.13	0.39	0.74

Movement toward the Gulf as winter and summer approach could be temperature related, *i.e.*, deep water sought to avoid temperature extremes. However, the pre-summer movement may also reflect a spawning migration. Ripe trout have been caught in the surf zone from June through August (Overstreet 1983, TPWD unpublished data), and trout larvae have been caught in bay-gulf passes on incoming tides in this same period (Overstreet

1983, Allshouse 1983). However, similar catches of adults and larvae have also been made in bays (Pearson 1929, Guest and Gunter 1958, Tabb 1961). One hundred percent survival of eggs and newly hatched larvae was predicted between 23.1° and 32.9° C over a salinity range of 18.6 to 37.5‰ (Taniguchi 1980), conditions which exist in the Gulf off the upper Texas coast in summer (TPWD unpublished data). Subsequent return to the upper reaches of bays after winter and summer may reflect a return to more suitable environmental conditions or may be related to food availability.

The apparent cyclic movement of trout also needs additional verification. The model for the relationship between time and distance traveled developed in this study explained only 15–36% of the variation in movement, indicating the model does not precisely describe the relationship. This is consistent with results of McEachron and Matlock (1980). Additional information on sex, age, maturity, and environmental variables may increase the amount of variation in movement explained, but these data will be difficult to obtain. Perhaps ultrasonic tags could be used to test the above hypothesis.

The potential existence of within-bay sub-groups has management implications. If growth and mortality vary among these groups, then some regulations (*i.e.*, size limits) may need to vary within bay systems and between bays and Gulf beaches where "stocks" may mix. At present, both growth and mortality rate information is inadequate to determine within-bay differences.

Growth rate calculated during this study was higher than published estimates. Annual growth of tagged fish 305 mm at release in Bastrop Bayou would be 211 mm (assuming 90 days of temperature 15° C). Tatum (1978) reported an annual growth of 105 mm in Mobile Bay, Alabama, and 67 mm in Aransas Bay, Texas, for similar size fish. Perret, Weaver, Williams, Johansen, McIlwain, Raulerson and Tatum (1980) presented data for Florida that indicated growth of about 30–60 mm for comparable fish.

Annual mortality of spotted seatrout is high throughout the Gulf of Mexico. Total annual mortality of Bastrop Bayou fish is 67–80%. In Alabama, mortality was 46–58% (Tatum 1978), and in Florida it was 44.7% (Iversen and Moffett 1962).

Spotted seatrout may remain in one "school" for an extended period of time. Initial work in Bastrop Bayou indicated that four fish tagged within 14 days were recaptured in one day by one fisherman at a location 122 km from the tagging site (McEachron and Matlock 1980). These fish had been free approximately 300 days. Similar results were obtained on three other occasions. In one case two tagged trout were recaptured on the same day at one location that had been released within 6 days of each other 941 and 935 days earlier. They were caught 31 km from the tagging site. "Subpopulation" units move, may or may not mix along the gulf beach; and this complicates management.

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LITERATURE CITED

ALLSHOUSE, W.C. 1983. The distribution of immigrating larval and postlarval fishes into the Aransas-Corpus Christi Bay complex. M.S. Thesis, Corpus Christi State University, Corpus Christi, Texas. 118 pp.

ANONYMOUS. 1983. Saltwater finfish research and management in Texas. A report to the Governor and the 68th Legislature. Texas Parks and Wildlife Department. 49 pp.

COLURA, R.L., C.W. PORTER and A.F. MACIOROWSKI. 1984. Preliminary evaluation of the scale method for describing age and growth of spotted seatrout, *Cynoscion nebulosus*, in the Matagorda Bay system, Texas. *Management Data Series. Texas Parks and Wildlife Department, Coastal Fisheries Branch.* No. 57. 17 pp.

DRAPER, N.R. and H. SMITH. 1966. *Applied Regression Analysis*. John Wiley and Sons, Inc., New York. 407 pp.

GREEN, A.W., G.C. MATLOCK and J.E. WEAVER. 1983. A method for directly estimating the tag-reporting rate of anglers. *Transactions of the American Fisheries Society.* 112:412–415.

GUEST, W.C. and G. GUNTER. 1958. The seatrout or weakfishes (genus *Cynoscion*) of the Gulf of Mexico. *Technical Summary. Gulf States Marine Fisheries Commission.* No. 1. 40 pp.

GUNTER, G. 1945. Studies on marine fishes of Texas. *Publications of the Institute of Marine Science, University of Texas.* 1(1):1–190.

INGLE, R.M., R.F. HUTTON and R.W. TOPP. 1962. Results of the tagging of salt water fishes in Florida. *Technical Series. Florida State Board of Conservation, Marine Laboratory.* 38. 57 pp.

IVERSEN, E.S. and A.W. MOFFETT. 1962. Estimation of abundance and mortality of a spotted seatrout population. *Transactions of the American Fisheries Society.* 91(4):395–398.

_____ and D.C. TABB. 1962. Subpopulations based on growth and tagging studies of spotted seatrout, *Cynoscion nebulosus*, in Florida. *Copeia.* 3:544–548.

MAHOOD, R.D. 1974. Seatrout of the genus *Cynoscion* in coastal waters of Georgia. *Contribution Series. Georgia Department of Natural Resources, Game and Fish Division, Coastal Fisheries Office.* No. 26. 35 pp.

McEACHRON, L.W. 1980. Gulf pier and jetty finfish catch statistics for the Gulf waters of Texas, September 1978–August 1979. *Management Data Series. Texas Parks and Wildlife Department, Coastal Fisheries Branch.* No. 11. 20 pp.

_____ and A.W. GREEN. 1984. Weekend sportboat fisherman finfish catch statistics for Texas bay systems, May 1974–May 1983. *Management Data Series. Texas Parks and Wildlife Department, Coastal Fisheries Branch.* No. 59. 138 pp.

_____ and G.C. MATLOCK. 1980. Movement of spotted seatrout, *Cynoscion nebulosus*, tagged in Bastrop Bayou, Texas. *Annual Proceedings of the Texas Chapter, American Fisheries Society.* 3:64–82.

MILES, D.W. 1950. The life histories of the seatrout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus. Report, Annual. Texas Game, Fish, and Oyster Commission, Marine Laboratory.* 1949–1950. 38 pp.

MOFFETT, A.W. 1961. Movements and growth of spotted seatrout, *Cynoscion nebulosus* (Cuvier), in west Florida. *Technical Series. Florida Board of Conservation.* No. 36:1–15.

NATIONAL MARINE FISHERIES SERVICE. 1980. Fisheries of the United States, 1979. *Current Fishery Statistics.* April 1980.

_____. 1982. Fisheries of the United States, 1981. *Current Fishery Statistics No.* 8200. April 1982.

OSBURN, H.R., G.C. MATLOCK and A.W. GREEN. 1982. Red drum (*Sciaenops ocellatus*) movement in Texas. *Contributions in Marine Science.* 25:85–87.

OVERSTREET, R.M. 1983. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus*, in Mississippi. *Gulf Research Reports, Supplement.* 1:1–43.

PEARSON, J.C. 1929. Natural history and conservation of redfish and other commercial Sciaenids on the Texas coast. *Bulletin of the Bureau of Fisheries.* 44: 129–214.

PERRET, W.S., J.E. WEAVER, R.O. WILLIAMS, P.L. JOHANSEN, R.D. McILWAIN, R.C. RAULERSON, and W.M. TATUM. 1980. Fishery profiles of red drum and spotted seatrout. Gulf States Marine Fisheries Commission. April 1980.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada.* **191.** 382 pp.

SIMMONS, E.G. 1951. Fish trap investigation. *Report, Annual. Texas Game, Fish, and Oyster Commission, Marine Laboratory.* 1950–1951:1–23.

SOKAL, R.F., and F.J. ROHLF. 1969. *Biometry.* W. H. Freeman, San LLFrancisco, California. 776 pp.

SPRINGER, V.G. and J. PIRSON. 1958. Fluctuations in the relative abundance of sport fishes as indicated by the catch at Port Aransas, Texas 1952–1956. *Publications of the Institute of Marine Science, University of Texas.* **5**: 169–185.

TABB, D.C. 1961. Contribution to the biology of the spotted seatrout, *Cynoscion nebulosus* (Cuvier), of east-central Florida. *Technical Series. Florida State Board of Conservation.* **35.** 24 pp.

TANIGUCHI, A.K. 1980. Abstract: Effects of salinity, temperature and food abundance upon survival of spotted seatrout eggs and larvae. p. 16. In *Proceedings: Colloquium on Biology and Management of Red Drum and Seatrout.* October 19–20. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

TATUM, W.M. 1978. Spotted seatrout (*Cynoscion nebulosus*) age and growth: data from annual fishing tournaments in coastal Alabama, 1964–1977. pp. 89–92. In *Proceedings: Colloquium on Biology and Mangement of Red Drum and Seatrout.* October 19–20. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

TRENT, L. 1976. Evaluation of the marine recreational fisheries in the northwestern Gulf of Mexico from Port Aransas to Port Isabel, Texas 1975–1976. In Environmental Studies of the South Texas Outer Continental Shelf, 1975 addendum to: Vol. I. Plankton and Fisheries. NOAA Final Report to Bureau of Land Management, Interagency Agreement No. 08550-IA5-19. 236 pp.

WEINSTEIN, M.P. 1975. Electrophoretic investigation of the Gulf of Mexico and Atlantic Ocean seatrouts of the genus *Cynoscion*, with special reference to the population structure of the spotted seatrout (*Cynoscion nebulosus*). Ph.D. Dissertation, Florida State University, Tallahassee. 115 pp.

_____ and R.W. YERGER. 1976. Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion. Fisheries Bulletin.* **74(3)**:599–607.

WOHLSCHLAG, D.E. 1981. Natural factors affecting recruitment. pp. 177–189. In Henry Clepper (editor) *Marine Recreational Fisheries, 6.* Proceedings of 6th Annual Marine Recreational Fisheries Symposium, Sport Fishing Institute, Washington, D.C.

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FEEDING SELECTIVITY AND STANDING STOCKS OF *FUNDULUS GRANDIS* IN AN ARTIFICIAL, BRACKISHWATER POND, WITH COMMENTS ON *CYPRINODON VARIEGATUS*

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ABSTRACT

The gut contents of fish from naturally-reproducing populations of the dominant Gulf coast marsh cyprinodonts, sheepshead minnow (*Cyprinodont variegatus*) and gulf killifish (*Fundulus grandis*), living in an unmanaged, artificial, 0.1-ha earthen pond were examined periodically from October 3 to December 1, 1981. Biota was sampled from October 3 to April 12, 1982 in this pond and in a fish-free pond.

F. grandis (*N* 47) showed greatest feeding selectivity for larval grass shrimp and crab parts. Large fish consumed primarily crabs and algae; smaller fish ate fine substrate, plant material, and amphipods. *C. variegatus* of all sizes (*N* 10) consumed filamentous algae and fine substrates.

Major energy pools in the pond with fish were filamentous algae, small amphipods, molluscs and fish; and in the fish-less pond widgeon grass (*Ruppia maritima*), large crustaceans (gammarid amphipods and crabs), and molluscs. Pond biota supported approximately 12,800 *C. variegatus* (19.4 kg) and 1,100 *F. grandis* (4.8 kg). Phytoplankton production in the pond with fish was twice that in the fish-less pond. Widgeon grass occupied 30% of the fish-less pond, but was absent in the presence of fish. Several food items selectively eaten in the stocked pond were more abundant in the fish-less pond.

INTRODUCTION

Sheepshead minnow (*Cyprinodon variegatus*) and gulf killifish (*Fundulus grandis*) are the dominant cyprinodonts and shallow-water marsh fishes of the Gulf coast (Kilby 1955, Simpson and Gunter 1956). We have observed *C. variegatus* and *F. grandis*, in a similar fashion to the mummichog (*Fundulus heteroclitus*) of the East coast (Butner and Brattstrom 1960), moving onto the marsh with flooding tides to feed with the water's advance and returning on the outgoing tide to tidal streams. *F. grandis* has been reported to feed

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opportunistically on invertebrates, especially crustaceans and insects and their larvae, and on algae and higher plants; at larger sizes they may prey on other fishes. *C. variegatus* in contrast consumes primarily plant material and detritus (Springer and Woodburn 1960, Harrington and Harrington 1961, Forman 1966, Martin 1970, Ruebsamen 1972). In spite of the presumed influence of both species on the marsh, no studies examining their effects have been performed. Perschbacher (1985) has compared interactions of *F. grandis* with both the biotic and abiotic environments among populations fed in fertilized brackishwater ponds, fed in unfertilized ponds and unfed in fertilized ponds. *F. heteroclitus* interaction with the marsh environment has been the object of numerous studies (Prinslow, Valiela and Teal 1974; Vince, Valiela and Backus 1976; Baker 1978; Kelso 1979; Meredith and Lotrich 1979; Kneib and Stiven 1982). The widespread trapping of *F. grandis* in east Texas marshes for use as live bait along the Gulf coast (Perschbacher 1985) will have ecological implications if populations are reduced.

The availability of a pair of 0.1-ha brackishwater ponds with and without naturally reproducing populations of *C. variegatus* and *F. grandis* provided the opportunity for sampling of biota and diets; and harvest by draining yielded an approximation of the number of *C. variegatus* and *F. grandis* made available for mosquito control through construction of a refugia pond in a salt marsh. Harrington and Harrington (1961) noted cyprinodonts should receive primary consideration in natural control of salt-marsh mosquito populations. Their study of food habits of 16 species of Florida fish during 11 days (September 10–21) of marsh inundation and mosquito hatch revealed *F. grandis* consumed the greatest proportion of mosquito larvae and pupa (94.8% of the diet by volume), with *C. variegatus* (57.3%) fifth. By contrast, the diet of the mosquito fish (*Gambusia affinis*) consisted of only 78.7% mosquitoes. Cyprinodonts, especially *Fundulus* spp. are also mentioned frequently in a literature review of studies pertaining to the control of mosquitoes by fish (Gerberich 1946). This study reports findings on the feeding preferences of *F. grandis*, the standing stock of fishes in the pond, and the composition of pond flora and macrofauna with and without these fishes.

MATERIALS AND METHODS

A food preference study of *F. grandis* was conducted from October 3 to December 1, 1981 in ponds at the Cedar Bayou Electric Generating Station, east of Baytown, Texas. Gut contents of *F. grandis* and biota in a pond with fish (F) and biota of a pond without fish (NF) were sampled five times at 2-week intervals. Gut contents of several *C. variegatus* were examined on three of these occasions. Biota in both ponds were sampled an additional five times at 4-week intervals from December 15, 1981 to April 12, 1982. The earthen ponds, constructed in 1974, were 0.1 ha in surface area and 1-m average depth. Ponds were filled with bay water from the discharge canal of the electric generating plant. Water was passed through a 335 μm filter bag to exclude incoming fishes. The F pond had been left in a natural state for 2 years, following stocking with *F. grandis*. *C. variegatus* entered accidentally through the water system. No other fishes gained entry. The NF pond was drained, fish removed, and refilled in the spring of 1981, and left unmanaged. Filtered water was added only as needed to maintain the pond level. The steep pond banks of both ponds supported sparse stands of smooth cordgrass (*Spartina alterniflora*). Filamentous algae

(*Cladophora* sp.), growing in the edges of the F pond, and widgeon grass (*Ruppia maritima*), occupying an estimated 30% of NF pond, were the dominant macroflora. Each twice-monthly biotic sampling consisted of six determinations. A set of light and dark bottles were each incubated from 1100 hours to 1400 hours on clear days at 0.25 and 0.75 m depths in each pond. The two samples were averaged to estimate gross primary productivity. Phytoplankton in a 100 ml sample from each pond were sedimented for 1 week after being preserved with formalin. Several milliliters were placed on a slide and major genera recorded. Zooplankton were concentrated from 15 liters of subsurface water at dusk collected in a calibrated bucket and poured through a Wisconsin net (153 μm mesh). These samples were preserved in formalin, and organisms present in 5 or 10 ml subsamples, depending on density, counted. Benthic macrofauna were sampled in each pond by three Peterson grabs at progressively greater depth from shoreline to level bottom. The three samples were combined, sieved through a 600 μm screen, and remaining substrate and organisms preserved in formalin. Organisms were counted employing a binocular, dissecting microscope. To enumerate numerous organisms such as hydrobiid snails and corophiid amphipods, a subsample of at least 1 g of substrate plus invertebrates was examined. Both the entire sample and subsample were weighed to the nearest 0.01 g and weights used in calculating the relative abundance of a subsampled organism. Invertebrate nekton and epifauna were sampled above the bottom in each pond by three plankton net sweeps of 2-m length. The 243-μm mesh net was mounted on a 0.3 m diameter wire hoop with handle. Finally, about 10 *F. grandis* were trapped between 1600 and 1800 hours and frozen for stomach-content analysis. Diel sampling of fish for gut contents revealed that active feeding occurred during this time period (Perschbacher 1985). The fish were weighed and measured, and the first segment of the gut, hereafter called the stomach (Babkin and Bower 1928) was removed. Contents were identified and percent composition by volume estimated.

Feeding preferences were determined by the linear index of food selection (Strauss 1979)

$$L_1 = r_1 - p_1$$

where r_1 is the relative abundance of a species in the stomach and p_1 is the relative abundance of a species in pond samples. To facilitate comparison with volumetric abundances of gut contents, contribution of a species or group to pond biota was converted from a numerical to volumetric basis by determining size equivalency to adult water boatman (Corixidae). Adult water boatman (approximately 5 mm in length) were assigned a value of 1. Other species were assigned values based on their size relative to an adult water boatman as determined from a projected slide. Percent composition by volume of sampled pond biota was then determined per 1 m^3 of pond water.

Gut contents from anterior portions of the gut of 10 *C. variegatus* were examined fresh. Contents were identified and their relative volumes estimated. Few *C. variegatus* were sampled as they were not the emphasis of the study and were assumed to have a predominantly plant-substrate diet.

At the end of the biotic sampling, April 12, 1982, the ponds were drained and fish collected in a cage placed on the drain. Fish species were separated and total biomass determined. A 1.0 kilogram subsample was counted to determine numbers of each species from the F pond.

RESULTS

Salinity ranges during the diet study were 8.7–10.2 and 6.5–7.2‰ in the F and NF ponds, respectively. Water temperature at 0800–0900 hours ranged from 14.5° to 28.0° C in both ponds.

Mean gross primary productivity of F and NF ponds, respectively, was 1.2 and 0.6 mg O_2/liter/4 hour incubation during the diet study and 0.5 and 0.3 mg O_2/liter/4 hours from December 15 to April 12. Dominant phytoplanktors varied. The most frequently observed phytoplankton genus in the F pond was

Nitzschia, in 5 of the 10 samples from October through April. *Nannochloris* was a dominant in 2 of the first 5 samples. Noted once each were *Ochromonas, Amphora, Navicula,* and *Gymnodinium.* In the NF pond unidentified nannoplankton were most frequently observed (3 of 5 samples) in the first sampling period, and *Nitzschia* in the second sampling period (4 of 5 samples). Noted once each as abundant were *Tetraselmis, Navicula, Tabularia, Glenodinium, Gymnodinium* and *Prorocentrum.*

Zooplankton were scanty in both ponds during the diet study (Table 1). The NF pond supported higher numbers than the F pond, including both calanoid and harpacticoid copepods. The extensive beds of widgeon grass undoubtedly allowed harpacticoid copepods to persist high in the water column. Calanoid copepods were the dominant zooplanktors in both ponds.

Filamentous algae along the margins of the F pond sheltered large numbers of corophiid amphipods (Table 1). Widgeon grass in the NF pond harbored primarily gammarid amphipods and false mussels (*Mytilopsis leucophaeta*).

The benthos in both ponds was numerically dominated by hydrobiid snails, indicating low predation pressures by fish on this group (Table 1) and confirmed by diet selectivity (Fig. 1). Number of benthic individuals was highest with fish present.

F. Grandis stomachs averaged 37% full ($N = 47$). They selectively utilized available foods as reflected by the indices of food selection (L) (Fig. 1). Six of 14 animal food groups were highly selected for. Greatest preference was displayed for larval grass shrimp followed by crab parts. Although amphipods constituted the major prey organism by volume, protective masses of filamentous algae probably prevented utilization equal to biomass available. Fish were visibly and audibly observed feeding at the margins of the algae mats and the high consumption of algae by fish may in part represent efforts to capture amphipods. Large fish primarily consumed crab parts and algae, and small fish fed on substrate, plants, and amphipods (Table 2).

C. variegatus stomachs averaged 67% full ($N = 10$). The sampled fish, 26–42 mm SL, consumed by volume an average of 72% filamentous algae, 26% fine substrate, and 2% false mussel. A 38 mm SL fish had consumed a false mussel.

Total fish biomass in the F pond was 24.2 kg. *C. variegatus* composed 19.4 kg: 12,800 fish at an average weight of 1.51 g and *F. grandis* 4.8 kg: 1,100 fish at an average weight of 4.44 g.

DISCUSSION

C. variegatus and *F. grandis* together consumed, except for hard-shelled molluscs, the available and abundant plant and animal food spectrum in the F. pond. *F. grandis* were observed to be particularly adept at removing the legs of fiddler crabs. Had they been present, blue crabs (*Callinectes sapidus*) would have completed the suite of top aquatic marsh consumers as their preferred food is molluscs (Virnstein 1977).

TABLE 1

Mean number and percent of invertebrate groups taken during the feeding study (October 3 to December 1, 1981), and following the feeding study (December 15, 1981 to April, 1982) in artificial impoundments with and without fish.

Group	With fish				Without fish			
	10/3/81-12/1/81		12/15/81-4/12/82		10/3/81-12/1/81		12/15/81-4/12/82	
	Number	(%)	Number	(%)	Number	(%)	Number	(%)
I. Zooplankton samples (Mean no./liter)								
Calanoid copepods	0.5	(16.1)	28.5	(75.2)	10.1	(51.8)	44.4	(87.6)
Nauplii	2.5	(80.6)	1.5	(4.0)	2.1	(10.8)	3.6	(7.1)
Polychaete larvae	0.1	(3.2)	0.2	(0.5)	0.1	(0.5)	0.9	(1.8)
Harpacticoid copepods			0.1	(0.2)	7.2	(36.9)	0.8	(1.6)
Amphipod zoea			7.6	(20.0)			0.9	(1.8)
Crab zoea							0.1	(0.2)
Grass shrimp larvae			0.1	(0.2)				
Total	3.1	(100.0)	38.0	(100.0)	19.5	(100.0)	50.7	(100.0)
II. Sweep samples (Mean no./3 sweeps)								
Corophiid amphipods	373.8	(95.8)	24.6	(58.0)	6.0	(10.8)		
Gammarid amphipods	0.8	(0.2)			41.4	(74.7)	99.6	(42.2)
Grass shrimp adults	8.6	(2.2)	8.2	(19.3)	0.2	(0.4)	3.8	(1.6)
False mussels	5.8	(1.5)	8.8	(20.7)	0.6	(1.2)	128.9	(54.6)
Mayfly nymphs			0.4	(0.9)	0.6	(1.2)	0.6	(0.2)
Damselfly nymphs	0.6	(0.2)	0.2	(0.5)	0.8	(1.4)		
Fiddler crabs	0.4	(0.1)			1.4	(2.5)	1.6	(0.7)
Water boatman	0.2	(T)			3.8	(7.0)	0.8	(0.3)
Dysticid beetles			0.2	(0.5)	0.4	(0.8)		
Total	390.2	(100.0)	42.4	(100.0)	55.4	(100.0)	235.9	(100.0)
III. Benthic samples (Mean no./m^2)								
Hydrobiid snails	16,885.0	(92.5)	9,556.0	(86.3)	12,625.0	(96.7)	1,723.1	(48.6)
Ostracods							1,471.7	(41.5)
Corophiid amphipods	895.9	(4.9)	1,078.3	(9.7)	15.0	(0.1)	2.9	(0.1)
Gammarid amphipods					177.6	(1.4)	123.1	(3.5)
Polychaetes	270.0	(1.5)	263.7	(2.4)	155.0	(1.2)	8.8	(0.2)
Macoma clams	120.0	(0.7)	128.9	(1.2)	115.0	(0.9)	52.7	(1.5)
Rangia clams	65.0	(0.3)	26.4	(0.2)	65.0	(0.5)	35.2	(1.0)
Hooked mussels	10.0	(T)						
Hydrophilid beetles			8.8	(0.1)	15.0	(0.1)		
Dysticid beetles			2.9	(T)			2.9	(0.1)
Mud crabs			2.9	(T)	5.0	(T)	2.9	(0.1)
Fiddler crabs			2.9	(T)			14.6	(0.4)
Chironomid larvae	5.0	(T)					108.4	(3.1)
Total	18,250.0	(100.0)	11,070.8	(100.0)	13,057.6	(100.0)	3,545.7	(100.0)

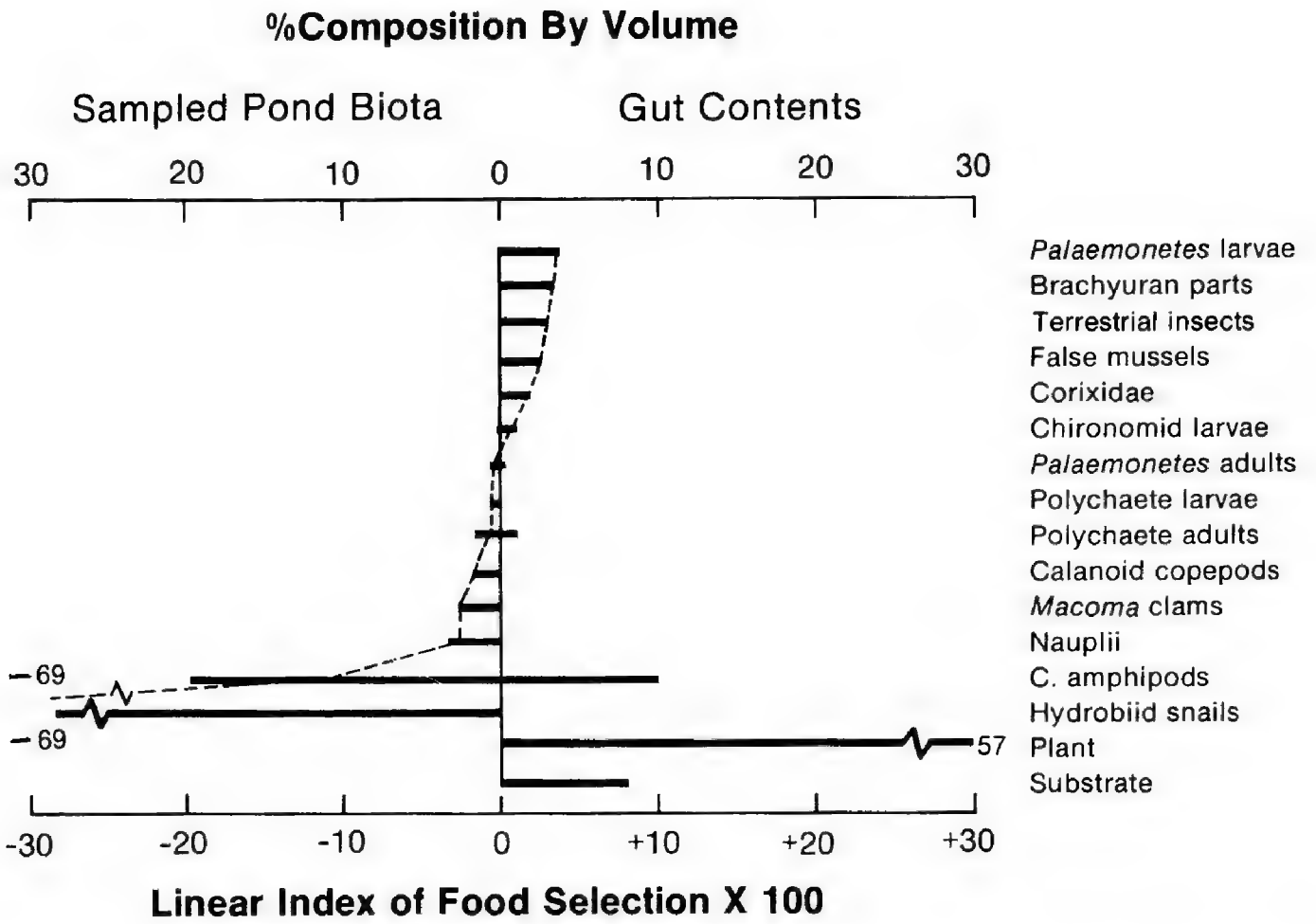

FIG. 1. Mean percent composition of volume of *F. grandis* gut contents and pond biota (bars) and individual (dashed line) and summed (ΣL) linear indices of food selection.

Primary production of phytoplankton in the F pond was higher than in the NF pond. Increased nutrient cycling and reduced coverage of competitive macroflora was proposed as the cause for the significantly elevated production in freshwater ponds with *Tilapia aurea* compared to unstocked ponds (Perschbacher 1975). Consumption of higher plant parts in greater measure than filamentous algae by *F. grandis* was unexpected (Table 2). In effect the spread of emergent plants would be reduced. Perhaps by reducing available cover for prey, as well as by the incidental nutrition from epifauna and epiflora, *F. grandis* obtains benefit. Emergent cover has been shown to sharply reduce foraging success of *F. heteroclitus* on amphipods (Vince *et al.* 1976).

Dominant biota in the F pond were filamentous algae, small amphipods, molluscs, and fish. *C. variegatus* comprised 92.1% by numbers and 80.2% by weight of the harvested fish and *F. grandis* the remaining 7.9% and 19.8%. The herbivore *C. variegatus* was the most abundant salt-marsh fish in several Gulf coast fish surveys (Kilby 1955, Simpson and Gunter 1956, Ruebsamen 1972). Mark and recapture estimates of *F. heteroclitus* standing stock in a tidal creek and marsh at high tide were 330 kg/ha (Valiela, Wright, Teal and Volkmen 1977), and 370 kg/ha in a tidal creek excluding the marsh (Meredith and Lotrich 1979). In the later estimate, standing stock is reduced if calculated at high tide when fish may swim onto the flooded marsh (Meredith and

TABLE 2

Mean stomach contents of *F. grandis* with food by size class and weighted means from all size classes.

	Fish size classes (SL mm)							
	41–45	46–50	51–55	56–60	61–65	66–70	Total	Mean
No. examined (empty)	2 (1)	2 (0)	5 (0)	22 (0)	13 (1)	3 (1)	47 (4)	
Mean fullness (%)	20.0	25.0	34.0	36.6	39.2	43.3		36.6
Food categories (% of total contents by volume)								
Crustaceans								
Harpacticoid copepods				0.9				0.4
Corophiid amphipods	10.0	55.0		16.2	0.4			10.9
Grass shrimp adults						10.0		0.4
Grass shrimp larvae			20.0	4.8				4.7
Crab parts					7.5	35.0		3.6
Insects								
Ants			6.0		0.4			0.8
Chironomid larvae				3.3				1.7
Water boatman				4.8		5.0		2.5
Unidentified insects	10.0		4.0	2.8	1.0	2.5		2.6
Annelids								
Polychaete adults					4.8			1.2
Molluscs								
False mussels		10.0		3.3	4.4			3.4
Macoma clams				0.5				0.2
Fish					3.3			0.9
Plants								
Filamentous algae		12.5	20.0	22.5	35.3	47.5		25.8
Higher plant parts		12.5	50.0	30.0	30.8			29.6
Plant seeds		10.0		1.9				1.3
Fine substrate	40.0			8.6	10.4			8.0
White stones	40.0							0.9

Lotrich 1979). These studies and ours (242 kg/ha in the F pond of *C. variegatus* plus *F. grandis)* indicate the potential biomass of fishes, of which *C. variegatus* and *F. grandis* would be the major components, that would be supported in a marsh impoundment for mosquito control. In the NF pond, dominant organisms were widgeon grass, large crustaceans (gammarid amphipods and crabs), and molluscs.

In addition to their effectiveness in exploiting the marsh, cyprinodonts are important in exporting energy from the marsh. *F. heteroclitus* productivity has been estimated at up to twice the biomass of standing stock with the differences indicative of intense predation by birds and other fishes (Valiela *et al.* 1977, Meredith and Lotrich 1979). Gulf marshes are frequented by numerous piscivorous birds and predatory fishes, such as southern flounder (*Paralichthys lethostigma*), red drum (*Sciaenops ocellatus*) and spotted sea trout (*Cynoscion nebulosus*) (Gunter 1967), and similar cyprinodont productivity-standing stock relationships are expected. Trapping of *F. grandis* as bait from localized marshes along the Gulf coast, especially in Alabama and Texas, is extensive, and its depletion may result in reduced cropping of marsh

invertebrates and flora. In these areas gamefish (*i.e.*, southern flounder) and piscivorous birds may decline and marsh mosquitos may increase.

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LITERATURE CITED

BABKIN, B.P. and D.J. BOWIE. 1928. The digestive system and its function in *Fundulus heteroclitus*. *Biological Bulletin*. 54:254–277.

BAKER, A.M. 1978. Foraging patterns of three sympatric killifish. *Copeia*. 78(3):383–309.

BUTTNER, A. and G.H. BRATTSTROM. 1960. Local movement in *Menidia* and *Fundulus*. *Copeia*. 1960:139–140.

FORMAN, W.W. 1966. The ecology of the Cyprinodontidae (Pisces) of Grand Terre Island, Louisiana. M.S. Thesis, Louisiana State University, Baton Rouge.

GERBERICH, J.B. 1946. An annotated bibliography of papers relating to the control of mosquitoes by the use of fish. *American Midland Naturalist*. 36:87–131.

GUNTER, GORDON. 1967. Some relationships of estuaries to the fisheries of the Gulf of Mexico. pp. 621–638. In G.H. Lauff (ed.) *Estuaries*. Publication 83, AAAS, Washington, D.C.

HARRINGTON, R.W. and E.S. HARRINGTON. 1961. Food selection among fishes invading a high subtropical saltmarsh: from onset of flooding through the progress of a mosquito brood. *Ecology*. 42:645–666.

KELSO, W.E. 1979. Predation on soft-shell clams, *Mya arenaria*, by the common mummichog, *Fundulus heteroclitus*. *Estuaries*. 2(4):249–254.

KILBY, J.P. 1955. Fishes of two Gulf coast marshes of Florida. *Tulane Studies in Zoology*. 2:176–247.

KNEIB, R.T. and A.E. STIVEN. 1982 Benthic invertebrate responses to size and density manipulations of the common mummichog, *Fundulus heteroclitus*, in a intertidal saltmarsh. *Ecology*. 63(5):1518–1532.

MARTIN, F.D. 1970. Feeding habits of *Cyprinodon variegatus* (Cyprinodontidae) from the Texas coast. *The Southwestern Naturalist*. 14:368–369.

MEREDITH, W.H. and V.A. LOTRICH. 1979. Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). *Estuarine and Coastal Marine Science*. 8:99–118.

PERSCHBACHER, P.W. 1975. The effect of an herbivorous fish, *Tilapia aurea* (Steindachner), on the phytoplankton community of fertilized ponds. M.S. Thesis, Auburn University, Auburn, Alabama.

_____. 1985. Interactions between cultured Gulf killifish *Fundulus grandis* and the brackishwater environment: bionomic and economic considerations. Ph.D. Dissertation, Texas A&M University, College Station.

PRINSLOW, T.E., I. VALIELA, and J.M. TEAL. 1974. The effect of detritus and ration size on the growth of *Fundulus heteroclitus* (L.). *Journal of Experimental Marine Biology and Ecology*. 16:1–10.

RUEBSAMEN, R.N. 1972. Some ecological aspects of the fish fauna of a Louisiana intertidal pond system. Master's Thesis, Louisiana State University, Baton Rouge.

SIMPSON, D.F. and G. GUNTER. 1956. Notes on habitats, systematic characters and life histories of Texas saltwater cyprinodonts. *Tulane Studies in Zoology*. 4:115–134.

SPRINGER, V.C. and K.D. WOODBURN. 1960. An ecological study of the Tampa Bay area. *Florida State Board of Conservation. Marine Laboratories, St. Petersburg. Professional Paper Series.* Number 1.

STRAUSS, R.L. 1979. Reliability estimates for Ivlev's electivity index, for forage ratio and a proposed linear index of food selection. *Transactions of the American Fisheries Society.* 108:344–352.

VALIELA, I., J.E. WRIGHT, J.M. TEAL and S.B. VOLKMEN. 1977. Growth, production and energy transformations in the salt-marsh killifish *Fundulus heteroclitus. Marine Biology.* 40:135–144.

VINCE, S., I. VALIELA and N. BACKUS. 1976. Predation by the salt-marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. *Journal of Experimental Marine Biology and Ecology.* 23:255–266.

VIRNSTEIN, R.W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology.* 58:1199–1217.

Contributions in Marine Science. (1986) Vol. 29:113–130.

STABLE ISOTOPIC STUDIES ON CHITIN. II. THE $^{13}C/^{12}C$ AND $^{15}N/^{14}N$ RATIOS IN ARTHROPOD CHITIN

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ABSTRACT

The nitrogen and carbon stable isotope ratios of chromatographically purified D-glucosamine hydrochloride from chitin in exoskeletons of more than 70 arthropod species from 59 geographical locations are presented. The isotopic ratios of chitin from different body parts of lobster and from new and old carapaces of individual crustaceans were found to vary non-systematically by small amounts. The isotopic variability of chitin from individuals within crustacean populations showed no dependence on sex or age if growth was not accompanied by shifts in diet. The $\delta^{13}C$ values of glucosamine from marine arthropods are, on average, 9.1 per mil less negative than those from arthropods in the terrestrial environment. The $\delta^{15}N$ values do not show distinct differences between marine and terrestrial specimens. Anthropogenic coastal pollution causes large variations in $\delta^{15}N$ values, while $\delta^{13}C$ values of chitin from animals living in polluted environments tend to be more negative due to the influx of ^{13}C-depleted terrigenous biomass into the marine environment. The $\delta^{15}N$ values of glucosamine from marine crustaceans were found to become more positive with increasing trophic level.

INTRODUCTION AND METHODS

Stable isotope ratios of carbon and nitrogen in different types of biomass have been used in many ecological, environmental and physiological studies. Carbon isotopic analysis has found application in studies of food webs, sediments, and seston to shed light on carbon flow patterns in marine, estuarine, riverine, and lacustrine ecosystems (for reviews see Fry and Sherr 1984, Deines 1980). Stable nitrogen isotope ratios have proven useful as trophic indicators in offshore systems (Rau 1981), as discriminating parameters to resolve marine *versus* terrestrial diets (Schoeninger, DeNiro and Tauber 1983; Schoeninger and DeNiro 1984; Mariotti, Letolle and Sherr 1983;

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Mariotti, Lancelot and Billen 1984), and as tracers for the influence of sewage on marine food webs (Rau, Sweeney, Kaplan, Mearns and Young 1981).

In nearly all of these studies, bulk biomass or whole tissues such as muscle, which are chemically heterogeneous materials, were used as substrates for isotopic analysis. Different biochemical fractions, such as amino sugars, amino acids, lipids, etc., may show large isotopic differences within an organism (DeNiro and Epstein 1978, 1981; Galimov 1980; Macko, Estep, Hare and Hoering 1983; Miller, Orr, Fritz, Downer and Morgan 1984; Tieszen, Boutton, Tesdahl and Slade 1983). These intrinsic isotopic heterogeneities will produce noise when isotope ratios of individuals with different chemical compositions are compared. This picture becomes even more complicated when comparative measurements on different species, with even more heterogeneous chemical and isotopic compositions among biochemical components, are concerned.

Such isotopic noise can be avoided by utilizing a well characterized and purified chemical substance rather than bulk biomass. Using bone collagen, Schoeninger and DeNiro (1984) were able to resolve isotopic differences related to diet among a variety of vertebrates in different ecosystems. In the case of floral organic matter, the use of cellulose rather than total biomass as a substrate for isotopic analysis brought a substantial improvement in analytical precision and has allowed fruitful applications in paleoclimatology (Epstein, Yapp and Hall 1976).

Chitin, one of the most abundant biopolymers, is present in the organic matrices of exoskeletons of a wide range of animal classes, as well as in fungi and some other lineages (Muzzarelli 1977). In particular, its availability from Arthropoda, Annelida and certain Mollusca, to name the larger phyla, make it a potentially valuable substrate for stable isotope studies on organisms in aquatic and terrestrial environments. It has been shown in previous studies (Schimmelmann 1985, Schimmelmann and DeNiro 1986a) that the reproducibility and interspecies comparability of stable isotope data from chitin can be increased by utilizing chromatographically purified D-glucosamine ("deacetylated chitin monomer") in its hydrochloride form (GlcN•HCl) instead of macromolecular chitin isolates, which may still be contaminated by covalently bonded proteinaceous compounds or may show compositional and isotopic heterogeneities due to isotopic effects related to the methods of preparation that were used. In this study, the chitins of more than 70 species of recent Crustacea, Insecta and Merostomata were processed for the measurements of the stable isotope ratios of carbon and nitrogen in GlcN•HCl. The objectives of this research were to provide basic understanding of the isotopic features of one of the most abundant and economically important biopolymers and to establish a data base for interpretations of stable isotope ratios in modern, archaeological and fossil chitins that will allow for investigation of new aspects of environmental and ecological research and for novel approaches in paleoclimatology, paleoecology and archaeology.

All arthropod specimens and sampling locations are shown in the Appendix. Additional information on these specimens is given by Schimmelmann

(1985). The processing of chitin and the determination of stable isotope ratios have been described by Schimmelmann (1985), Schimmelmann and DeNiro (1986a), and Northfelt, DeNiro and Epstein (1981). The isotopic results are expressed in the usual δ notation. The standards are the Peedee belemnite (PDB) carbonate for $\delta^{13}C$ values and atmospheric nitrogen (AIR) for $\delta^{15}N$ values. The precisions of the measurements, given as standard deviations of the means calculated for analyses of GlcN•HCl prepared from 10 aliquots of a single chitin sample, are ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

RESULTS AND DISCUSSION

I. Carbon and Nitrogen Isotope Ratios of Chitin GlcN•HCl, Muscle Biomass and Diet

We determined the relationship between the isotope ratios of GlcN•HCl and muscle biomass from individual species so that our results can be compared with those from studies based on analysis of muscle biomass. The results shown in Table 1 for an individual *Homarus americanus* (Northern lobster) and an individual *Ocypode ceratophtalmus* (ghost crab) provide another example of the large differences among isotope ratios of different biochemical components of an organism. A simple calculation based on the data shown in Table 1 illustrates that analysis of GlcN•HCl provides improved isotopic information compared with that obtained from analysis of whole biomass. Consider two organisms, one with 5% chitin and the other 20% chitin by weight in biomass. If the isotopic ratios of the chitin and the non-chitinous materials in both organisms differed in $\delta^{13}C$ and $\delta^{15}N$ values by the average differences between muscle biomass and GlcN•HCl shown in Table 1, the total biomass of the two organisms would differ by 0.3‰ in $\delta^{13}C$ values and 1.8‰ in $\delta^{15}N$ values. Moreover, the isotopic composition of the total biomass may reflect short-term variations in an animal's chemical composition (*e.g.* due to variation in gut contents or *postmortem* degradation of soft tissues),

TABLE 1

Carbon and nitrogen isotope ratios of muscle biomass and of D-glucosamine hydrochloride from chitin.

Species	Muscle Biomass $\delta^{13}C$(‰)	Muscle Biomass $\delta^{15}N$(‰)	GlcN•HCl $\delta^{13}C$(‰)	GlcN•HCl $\delta^{15}N$(‰)
Homarus americanus	−15.5	+12.0	−17.5	+0.5
Ocypode ceratophthalmus	−13.9	+7.7	−16.3	−4.6

whereas exoskeletal chitin is stable and its isotope ratios are not subject to transient perturbations.

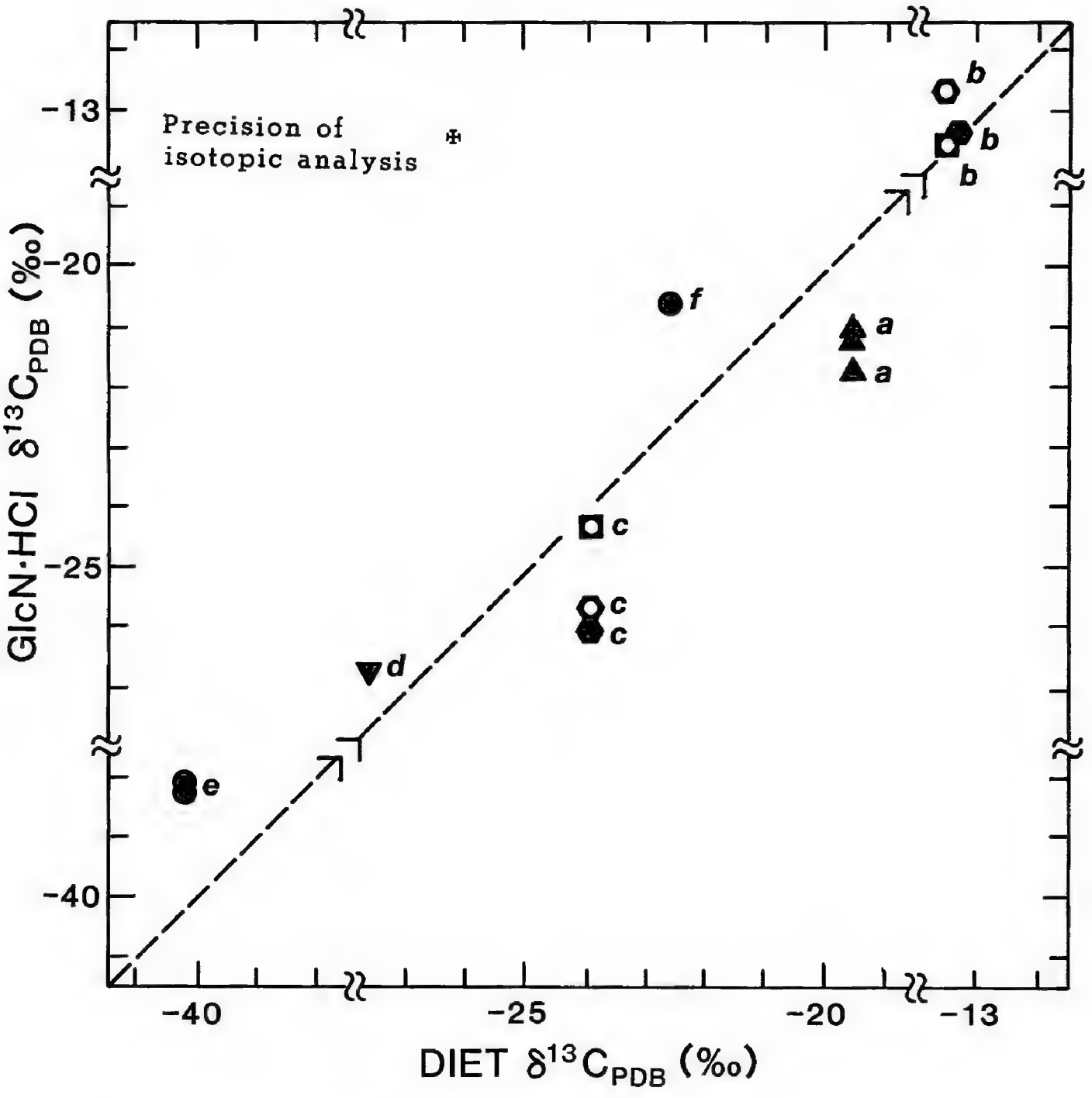

FIG. 1. $\delta^{13}C$ value of GlcN•HCl from chitin versus $\delta^{13}C$ value of diet.

Species: (▲) *Artemia salina* (brine shrimp);
(⬢) *Calliphora vicina* (blow fly);
(●) *Melanoplus sanguinipes* (grasshopper);
(■) *Musca domestica* (house fly);
(▼) *Oncopeltus fasciatus* (milkweed bug).

Open symbols indicate chitin from empty pupal cases; closed symbols indicate chitin from organisms.

Diets: (a) Mixture of 50% rice bran (*Oryza sativa*) and 50% corn bran (*Zea mays*);
(b) pork (*Sus acrofa*);
(c) horsemeat (*Equus caballus*);
(d) milkweed seeds (*Asclepias syriaca*);
(e) wheat seedlings (*Triticum aestivum*);
(f) corn seedlings (*Zea mays*).

Populations of five different species of arthropods were raised on controlled diets as described elsewhere (DeNiro and Epstein 1978, 1981; Schimmelmann 1985). Figs. 1 and 2 compare the isotopic ratios of the diets with the

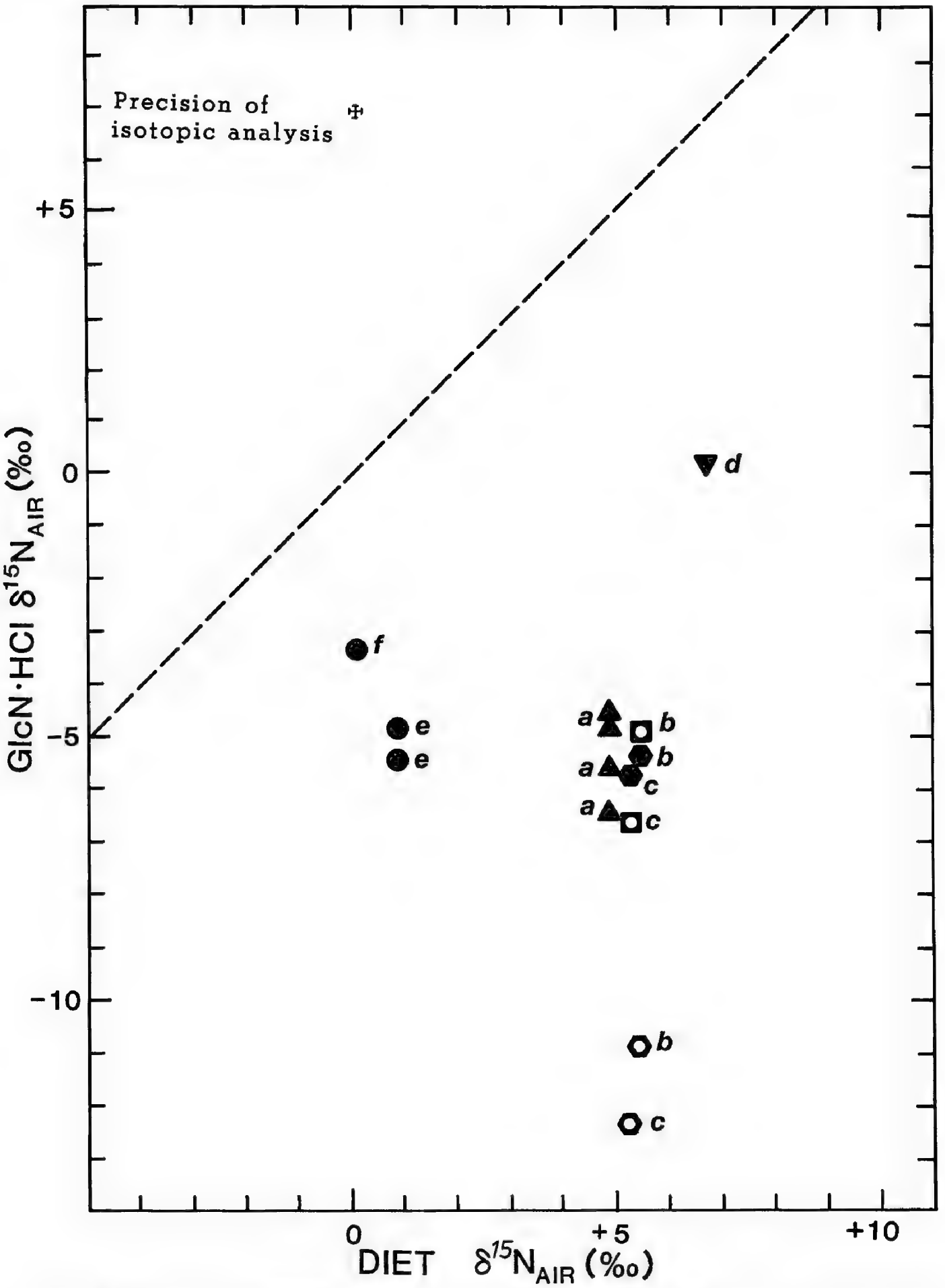

FIG. 2. $\delta^{15}N$ value of GlcN•HCl from chitin versus $\delta^{15}N$ value of diet. For explanation of symbols and identification of the diets refer to Fig. 1.

corresponding isotopic compositions of GlcN•HCl. There is a one-to-one correspondence between diet and GlcN•HCl $\delta^{13}C$ values (Fig. 1). The difference between the $\delta^{13}C$ value of GlcN•HCl and that of the diet range from -2.2‰ to $+2.1$‰, averaging 0.0 ± 1.5‰ for the 8 animal-diet combinations we analyzed. Such correlations have been observed between diet and whole biomass or macromolecular chitin in the same organisms by DeNiro and Epstein (1978).

In contrast, $\delta^{15}N$ values of GlcN•HCl do not bear a one-to-one relationship to the $\delta^{15}N$ values of the animals' diets (Fig.2). Differences in $\delta^{15}N$ values between GlcN.HCl and diet range from -17.5‰ to -3.3‰, averaging -9.5 ± 3.6‰. This observation is puzzling, in that DeNiro and Epstein (1981) observed good correspondence between diet $\delta^{15}N$ values and those of whole biomass or macromolecular chitin isolates for these same organisms. Also of interest is the observation that GlcN•HCl from the pupal cases of *Calliphora vicina*, a dipterid fly, has $\delta^{15}N$ values about 6‰ lower than those of GlcN•HCl from the adults that emerged from the cases. Additional work must be done to determine the biochemical basis for the strong depletion of ^{15}N in GlcN•HCl relative to diet nitrogen and for the variability of the relationship between the $\delta^{15}N$ values of diet and GlcN•HCl among different species and between different developmental stages of a single species.

II. Infraindividual Chitin Isotopic Variability

It is not always practical or possible to process the entire exoskeleton of an arthropod for the determination of stable isotope ratios in chitin. For example, in the case of archaeological or fossil samples, whole exoskeletons are rarely preserved. To evaluate the likelihood of introducing uncertainty into the measurements by processing only a part of an exoskeleton, the stable isotope ratios of five body sections (left manus; 4th and 5th pereopods; uropods; pleopods; and gastric, orbital, antennal, hepatic and branchial regions of the carapace) from a Northern lobster (*Homarus americanus*) were determined (Table 2). The mean stable isotope ratios for the five sections with their standard deviations and the respective ranges are:

$$\delta^{13}C = -17.5 \pm 0.2‰ \text{; range } 0.5‰ \text{ and}$$
$$\delta^{15}N = +0.5 \pm 0.5‰ \text{; range } 1.3‰.$$

Another aspect of infraindividual chitin variability is related to ecdysis, *i.e.* molting. In crustaceans, ecdysis is preceded, accompanied and followed by a variety of metabolic processes including partial leaching of the old cuticle and subsequent deposition of organic and inorganic materials in the new cuticle. The chitin content in the postmolt cuticle increases rapidly shortly after molting and continues to increase for many days (Vigh and Dendinger 1982, Kulkarni 1983, Koulish and Gould 1983). In order to study the effects of ecdysis on chitin isotope ratios, GlcN•HCl was prepared from the calcified old and soft new exoskeletons of a crayfish (*Oronectes limosus*), a shore crab

TABLE 2

Carbon and nitrogen isotope ratios of D-glucosamine hydrochloride from the chitins of five different body sections of a lobster, *Homarus americanus*.

Body section	$\delta^{13}C(‰)$	$\delta^{15}N(‰)$
Left manus	-17.7	+0.8
4th and 5th Pereopods	-17.2	+1.3
Uropods	-17.4	+0.2
Pleopods	-17.3	0.0
Gastric, orbital, antennal, hepatic, and branchial regions	-17.7	+0.3

(*Grapsus tenuicrustatus*) and three green crabs (*Carcinus maenas*) that were molting. The difference in the isotope ratios between the old and new exoskeletons (Table 3) of these individual specimens varied non-systematically, averaging

$$\Delta\delta^{13}C = +0.4 \pm 0.6\text{ ; range }1.5‰\text{ and}$$
$$\Delta\delta^{15}N = -1.0 \pm 1.9\text{ ; range }4.8‰.$$

It is of interest to note that the largest difference between old and new exoskeletons for $\delta^{13}C$ values is 1.3‰, while that for $\delta^{15}N$ values is 4‰. These values are similar to the differences between the $\delta^{13}C$ and $\delta^{15}N$ values of GlcN•HCl from pupal cases and adults of *Calliphora vicina* (Figs. 1, 2).

Consequently, isotopic data for GlcN•HCl from sections of exoskeletons or from molts of an individual crustacean can be expected to show intrinsic variability in the ranges given above. Variation in the magnitude of isotope effects associated with chitin biosynthesis together with changes in the isotopic ratios of the precursors of chitin available during an animal's lifetime probably account for our observations.

III. Chitin Isotopic Variability within Crustacean Populations

We determined the isotopic variability of chitin from individuals within populations and also studied the influences of age and sex.

First, the $\delta^{13}C$ and $\delta^{15}N$ values of ten male red swamp crayfish (*Procambarus clarkii*) were measured using the right claws of individuals whose carapace widths (*W*) were within ±10% of one another. The mean δ values for carbon and nitrogen together with their standard deviations and ranges are:

TABLE 3

Carbon and nitrogen isotope ratios of D-glucosamine hydrochloride from the chitins of old (shed) and new (postmolt) exoskeletons from crustacean individuals.

	Old carapace		New carapace	
	$\delta C(^{\circ}/_{oo})$	$\delta N(^{\circ}/_{oo})$	$\delta C(^{\circ}/_{oo})$	$\delta N(^{\circ}/_{oo})$
Oronectes limosus	-27.9	-3.5	-28.3	-4.3
Grapsus tenuicrustatus	-15.7	-2.4	-15.7	-1.4
Carcinus maenas	-16.9	-0.5	-16.7	+1.0
	-17.9	-0.9	-18.5	-1.5
	-18.0	-1.2	-19.3	+2.8

$$\delta^{13}C = -19.2 \pm 0.4‰ \text{; range } 1.5‰ \text{ and}$$
$$\delta^{15}N = +0.6 \pm 0.6‰ \text{; range } 1.9‰.$$

Three crustacean populations were sampled for the determination of isotopic variability due to size as measured by the width of carapace (W). The results for ghost crabs (*Ocypode ceratophtalmus*, wharf crabs (*Sesarma* sp.) and striped shore crabs (*Pachygrapsus crassipes*) are presented in Fig. 3. Age, as was estimated by the size of the crustacean, apparently does not have any systematic influence on the stable isotope composition in chitin from *Sesarma* sp. and *Pachygrapsus crassipes*. While the same is true for nitrogen isotope ratios in *Ocypode ceratophtalmus*, the $^{13}C/^{12}C$ ratio for this species shows a steady decline in all male individuals up to $W = 23$ mm (the sex of the smallest individuals could not be determined). A linear regression analysis of the six data points yields the relationship

$$\delta^{13}C = \left[\frac{0.18‰}{mm}\right]\left[W \text{ (in mm)}\right] + 18.9‰ \text{; } R^2 = 0.98.$$

The explanation for the presence of this relationship in *O. ceratophtalmus* and its absence in the other two species probably lies in the feeding behavior of individuals of different ages. In the cases of the non-burrowing wharf and striped shore crabs, our field observations indicated that all generations share the same habitat and diet. In contrast, ghost crabs locate their burrows further inland and higher above the water table with increasing age and size (Cott 1929, Crane 1941) and consequently are subject to a concomitant dietary shift from predominantly marine toward terrigenous biomass, which would produce the shift in GlcN•HCl $\delta^{13}C$ values we observed (see section IV below). The observed constancy of the $\delta^{15}N$ values over age for this species may be due to local nitrogen isotopic similarity between marine and terrigenous diets. For

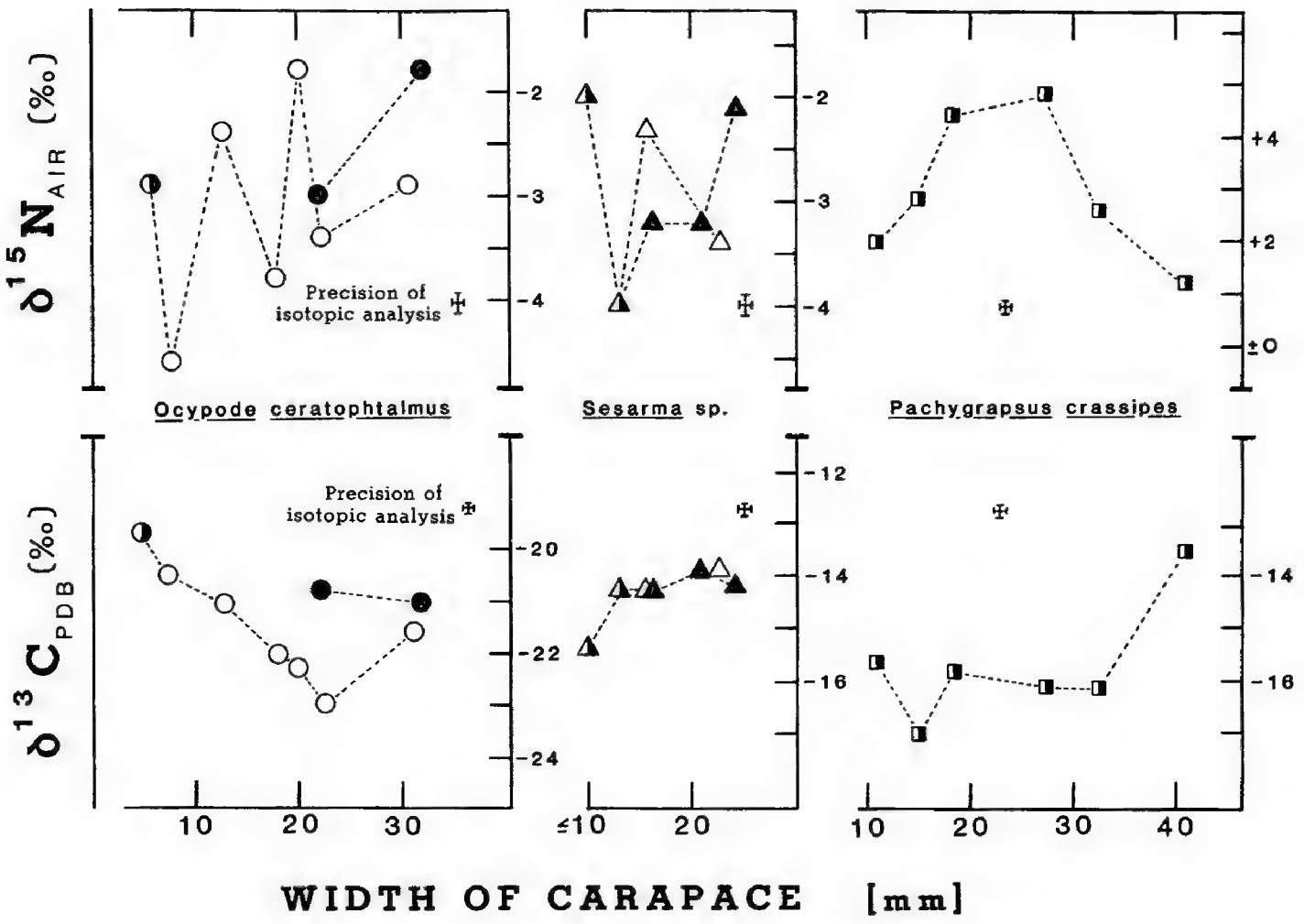

FIG. 3. Isotopic variation among individuals of crustacean populations: ghost crabs (*Ocypode ceratophtalmus*) sampled at Papawei Pt. (Maui); wharf crabs (*Sesarma* sp.) sampled at Pt. Allen Harbor (Kauai); striped shore crabs (*Pachygrapsus crassipes*) sampled at Palos Verdes (Los Angeles). Explanation of symbols: ○ and △ : male; ● and ▲ : female; ◑, ◭ and ◨ : sex undetermined.

comparison, Minagawa and Wada (1984) found no systematic relationship between $\delta^{15}N$ values of soft tissues from mussels and age except that younger individuals displayed more variability than older ones. In contrast, Rau *et al.* (1981) reported more positive $\delta^{15}N$ values with increasing weight in fish.

The sex of a crustacean does not have a systematic influence on the stable isotopic composition of GlcN•HCl. For *Ocypode ceratophtalmus* (ghost crab, 1 pair), *Sesarma* sp. (wharf crab, 3 pairs), *Pachygrapsus crassipes* (striped shore crab, 1 pair), and *Hemigrapsus oregonensis* (yellow shore crab, 1 pair), the differences in carbon and nitrogen isotope ratios between males and females captured together (with W being equal to within ±10% do not show any trend (Table 4), and average

$$\Delta\delta^{13}C = -0.4 \pm 1.0‰ \text{ ; range } 2.8‰ \text{ and}$$
$$\Delta\delta^{15}N = -0.3 \pm 0.9‰ \text{ ; range } 2.2‰.$$

IV. Comparative Studies on Species from Various Locations

Environmental and climatic influences on $\delta^{13}C$ and $\delta^{15}N$ values of GlcN•HCl from arthropod chitins were evaluated using a large variety of arthropods

TABLE 4

Carbon and nitrogen isotope ratios of D-glucosamine hydrochloride from the chitin of male and female crustaceans of comparable sizes.

	Male		Female	
	δC(°/₀₀)	δN(°/₀₀)	δC(°/₀₀)	δN(°/₀₀)
Ocypode ceratophthalmus	-21.6	-2.9	-21.0	-1.8
Sesarma sp.	-13.9	-3.4	-14.2	-2.1
	-14.3	-2.3	-14.3	-3.2
	-13.9	-3.4	-13.9	-3.2
Pachygrapsus crassipes	-16.6	0.0	-16.7	+1.0
Hemigrapsus oregonensis	-17.7	+5.8	-15.2	+5.0

sampled in the Hawaiian Islands, the Caribbean, North and South America and Europe.

IV. 1. Marine *versus* terrestrial organic matter

The carbon isotopic difference between terrestrial plant material ($\delta^{13}C$ values averaging −26‰) and organic matter of marine origin (*i.e.* phytoplankton with δ^{13} C values of *ca.* −21‰) has been used to trace the influence of land-derived organic carbon in the marine environment (reviewed by Fry and Sherr 1984). The isotopic distinction between average terrigenous and marine organic carbon sources is clearly reflected in the $\delta^{13}C$ values of GlcN•HCl from arthropod chitin and can be used for the characterization of habitat and diet. Figure 4 contains data for all sampling locations in terms of average carbon and nitrogen stable isotope compositions for each species sampled in each location. The carbon stable isotope composition defines two distinct clusters of samples from marine and terrestrial environments. The mean $\delta^{13}C$ values for the two environments are:

$$\text{Marine} = -16.5 \pm 2.2‰ \text{ ; range } 9.1‰ \text{ ; } (n = 43) \text{ and}$$
$$\text{Terrestrial} = -25.6 \pm 3.9‰ \text{ ; range } 17.6‰ \text{ ; } (n = 16).$$

The difference is statistically significant at the $P = 0.05$ level (two-tailed Student's *t* test).

Several authors report differences in $\delta^{15}N$ values between average terrigenous suspended organic matter and average marine suspended organic matter in estuarine and offshore systems (reviewed by Mariotti *et al.* 1984). However, the $\delta^{15}N$ values of GlcN•HCl from marine *versus* terrestrial locations in Fig. 4 do not distinguish between the two environments. The averages are:

Marine = -1.1 ± 2.8‰ ; range 13.8‰ ; ($n = 43$) and
Terrestrial = -1.7 ± 2.7‰ ; range 11.7‰ ; ($n = 16$).

Subdividing the samples on the basis of various categories of marine and terrestrial environments, which is done in Fig. 5, does not clarify the basis for the lack of separation between marine and terrestrial $\delta^{15}N$ values. From these data, we suggest that the geochemical and biogeochemical pathways of nitrogen in littoral and terrestrial ecosystems are not as clearly understood as has been heretofore assumed. A similar conclusion was reached by Mariotti *et al.* (1983) in a study of stable nitrogen and carbon isotopes in a Georgia salt marsh estuarine ecosystem. They stated: "$\delta^{15}N$ does not appear to be as useful as $\delta^{13}C$ because of larger and more variable fractionation of nitrogen isotopes as compared to carbon isotopes in both microbial and animal metabolism." The results discussed above in sections I and II also support this conclusion.

IV. 2. Pollution effects

Municipal and industrial anthropogenic sewage is generally depleted in ^{13}C relative to average oceanic biomass. Such sewage influx is especially intense

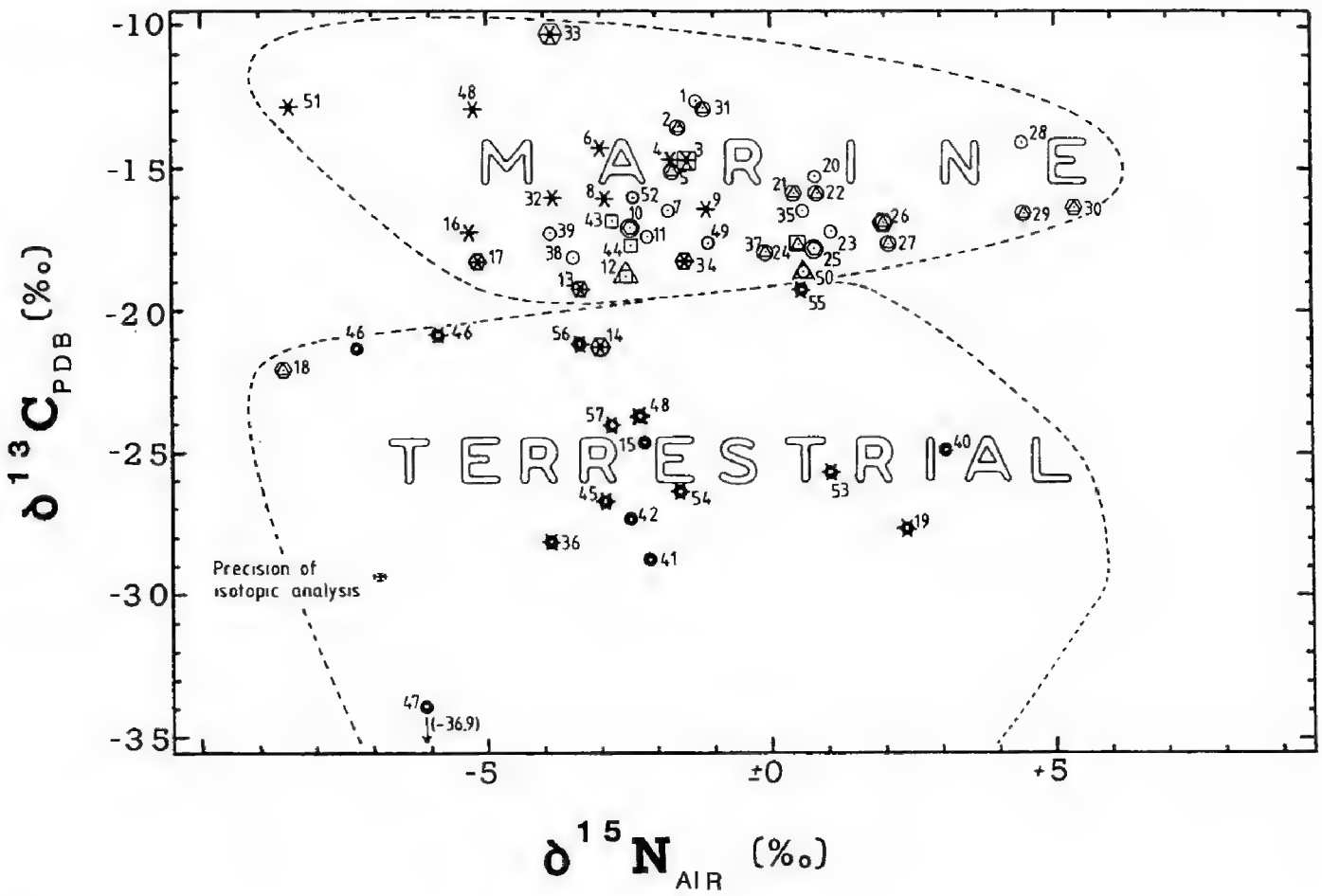

FIG. 4. $\delta^{13}C$ and $\delta^{15}N$ values of GlcN•HCl from chitin of marine and terrestrial arthropods. Each point represents the mean value for all species at one location, calculated using an average value for each species sampled. Locations are indicated by their numbers and are further characterized by the following symbols, which are combined in some cases:(✳) tropical marine; (⊙) littoral, non-tropical; (⊡) sublittoral/off-shore; (✿) terrestrial (crustaceans); (●) terrestrial (insects); (△) in or near large cities; (◎) subject to terrestrial biomass influx.

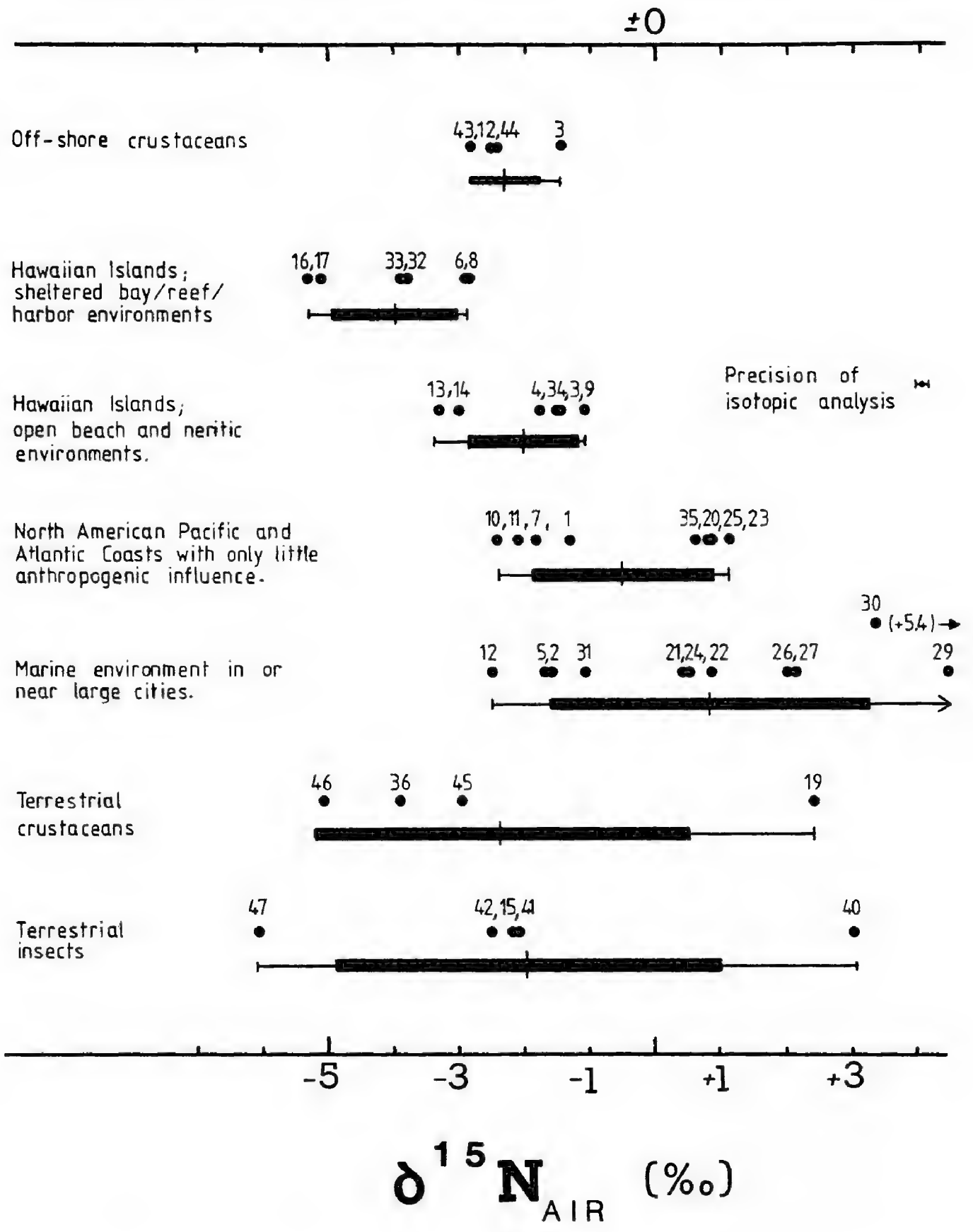

FIG. 5. $\delta^{15}N$ values of GlcN•HCl from chitin in arthropods sampled in various categories of marine and terrestrial environments. Each point represents the mean value for all species at a location, calculated using an average value for each species sampled. Locations are indicated by their numbers. The range, mean, and standard deviation for each group are indicated.

near San Pedro in the Los Angeles area (Rau *et al.* 1981). Figure 6 displays $\delta^{13}C$ and $\delta^{15}N$ values of GlcN•HCl from crustacean specimens collected in or near the sewage outfall area off San Pedro together with the data for crustaceans

collected in less polluted Southern Californian and Northern Baja Californian environments. The average $\delta^{13}C$ value of all measured crustaceans from San Pedro ($\delta^{13}C = -18.8‰$) is 3.6‰ more negative than the average of all other locations shown in Fig. 6. The $\delta^{15}N$ values in the polluted area tend to be more negative than those from the unpolluted areas. The combined plot of $\delta^{13}C$ *versus* $\delta^{15}N$ values shows no overlap of the two clusters. Statistical analysis of the observed mean isotopic differences between polluted and all other locations yields significance at the $P = 0.05$ level (one-tailed Student's t test). Our results are in good agreement with data on muscle tissue of *Sicyonia ingentis* (ridgeback prawn) caught in the same polluted location and in an unpolluted area (Rau *et al.* 1981), and with the results of a study by Fry,

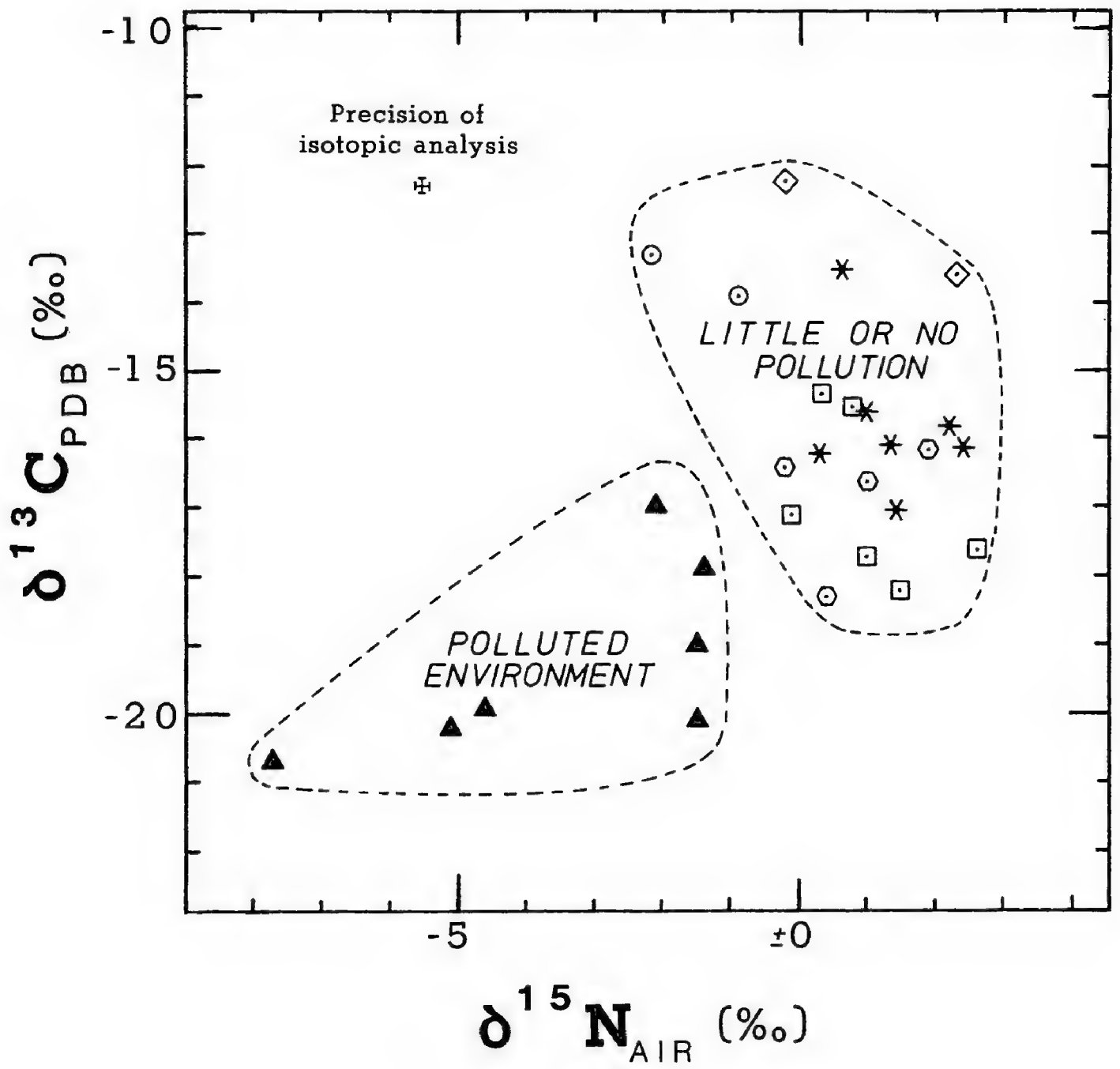

FIG. 6. Effects of pollution on $\delta^{13}C$ and $\delta^{15}N$ values of GlcN·HCl from chitin. Each point represents one marine crustacean sample obtained from:(▲) San Pedro; (⊡) Leo Carillo State Beach; (✳) Palos Verdes; (⊙) Dana Point; (⊙) San Diego; and (◇) Ensenada.

Anderson, Entzeroth, Bird and Parker (1984), who measured the muscle tissues of three different species of the genus *Sicyonia* from non-polluted areas in the Gulf of Mexico. In all cases, prawns from the polluted environment were found to display relatively more negative $\delta^{13}C$ values than specimens of the same genus from unpolluted areas. Moreover, the low $\delta^{15}N$ values measured for *Sicyonia* caught off San Pedro in this study compared with those from unpolluted areas correlate well with observations of $^{15}N/^{14}N$ ratios reported by Rau *et al.* (1981).

IV. 3. Trophic level effects

Minagawa and Wada (1984) reported a stepwise increase of the $\delta^{15}N$ values in whole biomass or muscle tissue with increasing trophic level of about 3.4 ± 1.1‰ per trophic level in intertidal ecosystems. Similar observations have been made for vertebrates using bone collagen as the substrate for isotopic analysis (Schoeninger and DeNiro 1984).

Measurements of $^{15}N/^{14}N$ ratios in crustacean GlcN•HCl from four different locations that involved sampling at different trophic levels are shown in Table 5. Our observations fit well into the picture outlined by Minagawa and Wada. The omnivorous and carnivorous species generally have GlcN•HCl $\delta^{15}N$

TABLE 5

Carbon and nitrogen isotope ratios of D-glucosamine hydrochloride from the chitin of arthropods feeding at different trophic levels.

Location / Species	Trophic Level	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)
Location #10, Coos Bay			
Idotea wosnesenskii	Scavenger	-16.9	-4.5
Circolana harfordi	Scavenger	-16.5	-2.3
Cancer magister	Omnivore	-17.7	-2.2
Hemigrapsus oregonensis	Omnivore	-17.6	-0.4
Location #11, Assateague Island			
Gammaridea	Scavenger	-17.0	-3.7
Emerita talpoida	Filter feeder	-16.2	-3.5
Cancer irroratus	Omnivore	-19.2	-0.6
Limulus polyphemus	Carnivore	-17.0	-0.2
Location #38, John O'Groat's			
Gammaridea	Scavenger	-19.4	-5.1
Carcinus maenas	Omnivore	-17.0	-1.8
Location #39, Balmacara			
Gammaridea	Scavenger	-17.3	-5.3
Carcinus maenas	Omnivore	-17.1	-2.3

values 3–4‰ more positive than those of scavenging and filter-feeding (herbivorous) species.

A smaller but significant correlation of increasing $\delta^{13}C$ value with trophic level has been reported by several authors (reviewed by Schoeninger and DeNiro 1984, Fry *et al.* 1984) but was not found in this study, as shown in Table 5.

CONCLUSIONS

The results reported here indicate yet again the usefulness of determining carbon and nitrogen isotope ratios in biologic material in order to answer ecological questions. The large number of species from different environments we analyzed permitted identification and statistical confirmation of various biological, ecological and anthropogenic factors that influence the $\delta^{13}C$ and $\delta^{15}N$ values of arthropod chitin. We have shown elsewhere (Schimmelmann, DeNiro, Poulicek, Voss-Foucart, Goffinet and Jeuniaux 1986) that the carbon and nitrogen isotope ratios of glucosamine do not suffer substantial alteration during *postmortem* events, such as biodegradation or heating, that cause partial destruction of chitin. Thus, we expect that isotopic analysis of glucosamine isolated from arthropod specimens that still contain chitin in spite of having no soft parts preserved (*e.g.* samples recovered from archaeological contexts) will permit useful paleoecological reconstruction when interpreted in light of the observations reported here. Furthermore, while the extra effort required to isolate glucosamine from chitin may not be warranted in situations in which analysis of whole biomass or muscle tissue provides carbon and nitrogen isotope data sufficiently sensitive to resolve the questions at hand, the climatic and additional dietary information recorded in the oxygen and hydrogen isotope ratios of glucosamine (Schimmelmann and DeNiro 1986b) will make it the substrate of choice for isotope analysis in many ecological applications.

ACKNOWLEDGMENTS

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LITERATURE CITED

COTT, H.B. 1929. The Zoological Society's expedition to the Zambesi, 1927: No. 3 Observations on the natural history of the racing-crab O*cypode ceratophtalma*, from Beira. *Proceedings of the Zoological Society of London, 1929*: 755–765.

CRANE, J. 1941. Eastern Pacific expeditions of the New York Zoological Society. XXIX. On the growth and ecology of brachyuran crabs of the genus *Ocypode*. *Zoologica.* 26:297–310.

DEINES, P. 1980. The isotopic composition of reduced organic carbon. pp. 329–406. In P. Fritz and J.C. Fontes, (eds.) *Handbook of Environmental Isotope Geochemistry, 1980.* Elsevier, Amsterdam.

DeNIRO, M.J. and S. EPSTEIN. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta.* 42:495–506.

_____ and _____. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta.* 45:341–351.

EPSTEIN, S., C.J. YAPP and J. HALL. 1976. The determination of the D/H ratio of non-exchangeable hydrogen in cellulose extracted from aquatic and land plants. *Earth and Planetary Science Letters.* 30:241–251.

FRY, B., R.K. ANDERSON, L. ENTZEROTH, J.L. BIRD and P.L. PARKER. 1984. ^{13}C enrichment and oceanic food web structure in the Northwestern Gulf of Mexico. *Contributions in Marine Science.* 27:49–63.

FRY, B. and E.B. SHERR. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater systems. *Contributions in Marine Science.* 27:13–47.

GALIMOV, E.M. 1980. $^{13}C/^{12}C$ in kerogen. pp 271–299. In B. Durand (ed.) *Kerogen. Insoluble Organic Matter from Sedimentary Rocks.* Editions Technip, Paris.

KOULISH, S. and R.M. GOULD. 1983. Autoradiographic and fine structural study of chitin deposition in the cuticle of a barnacle using [^{3}H]-D-glucosamine incorporation. *Tissue & Cell.* 15:749–760.

KULKARNI, K.M. 1983. Some changes in the biochemical composition of the sand crab, *Emerita holthuisi*, during molt cycle. *Comparative Physiology and Ecology.* 8:202–204.

MACKO, S.A., M.L.F. ESTEP, P.E. HARE and T.C. HOERING. 1983. Stable nitrogen and carbon isotopic composition of individual amino acids isolated from cultured microorganisms. *Annual Report of the Director of the Geophysical Laboratory, Carnegie Institution, Washington, D.C.* 82:404–410.

MARIOTTI, A., C. LANCELOT, and G. BILLEN. 1984. Natural isotopic composition of nitrogen as a tracer of origin for suspended organic matter in the Scheldt estuary. *Geochimica et Cosmochimica Acta.* 48:549–555.

MARIOTTI, A., R. LeTOLLE, and E. SHERR. 1983. Distribution of stable nitrogen isotopes in a salt marsh estuary. *Estuaries.* 6:304–305.

MILLER, R.F., G.L. ORR, P. FRITZ, R.G.H. DOWNER and A.V. MORGAN. 1984. Stable carbon isotope ratios in *Periplaneta americana* L., the American cockroach. *Canadian Journal of Zoology.* 63:584–589.

MINAGAWA, M. and E. WADA. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta.* 48:1135–1140.

MUZZARELLI, R.A.A. 1977. *Chitin.* Pergamon Press, Oxford.

NORTHFELT, D.W., M.J. DeNIRO, and S. EPSTEIN. 1981. Hydrogen and carbon isotopic ratios of the cellulose nitrate and saponifiable lipid fractions prepared from annual growth rings of a California redwood. *Geochimica et Cosmochimica Acta.* 45:1895–1898.

RAU, G.H. 1981. Low $^{15}N/^{14}N$ in hydrothermal vent animals: ecological implications. *Nature.* 289:484–485.

_____, R.E. SWEENEY, I.R. KAPLAN, A.J. MEARNS, and D.R. YOUNG. 1981. Differences in animal ^{13}C, ^{15}N and D abundance between a polluted and an unpolluted coastal site: likely indicators of sewage uptake by a marine food web. *Estuarine, Coastal and Shelf Sciences.* 13:701–707.

SCHIMMELMANN, A. 1985. Stable isotopic studies on chitin. Ph.D. Thesis. University of California at Los Angeles. 223. p.

_____ and M.J. DENIRO. 1986a. Stable isotopic studies on chitin I. Measurements on chitin/chitosan isolates and D-glucosamine hydrochloride from chitin. In R.A.A. Muzzarelli, C. Jeuniaux and G.W. Gooday (eds.) *Chitin in Nature and Technology.* Plenum Publishing Corp., New York, in press.

_____ and _____. 1986b. Stable isotopic studies on chitin III. The D/H and $^{18}O/^{16}O$ ratios in arthropod chitin. *Geochimica et Cosmochimica Acta.* (in press).

————, ————, M.POULICEK, M.F. VOSS-VOUCART, G. GOFFINET and C. JEUNIAUX. 1986. Isotopic composition of chitin from arthropods recovered in archaeological contexts as palaeoenvironmental indicators. *The Journal of Archaeological Science.* (in press).

SCHOENINGER, M. and M.J. DeNIRO. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta.* 48:625–639.

————, ————, and H. TAUBER. 1983. Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. *Science.* 220:1381–1383.

TIESZEN, L.L., T.W. BOUTTON, K.G. TESDAHL, and N.A. SLADE. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. *Oecologia.* 57:32–37.

VIGH, D.A. and J.E. DENDINGER. 1982. Temporal relationships of postmolt deposition of calcium, magnesium, chitin and protein in the cuticle of the Atlantic blue crab, *Callinectes sapidus* Rathbun. *Comparative Biochemistry and Physiology.* 72A:365–369.

Appendix: Locations and species sampled

Number	Location	Species sampled
1	San Onofre State Beach, Calif.	*Emerita analoga*
2	Mission Bay, California	*Pachygrapsus crassipes*
3	Maui Island, Hawaiian Islands	*Ula* sp.
4	Kapalua, Maui, Hawaiian Islands	*Forestia depressa* *Grapsus tenuicrustatus* *Leptodius sanguineus* *Lophopanopeus* sp. *Ocypode ceratophtalmus* *Percnon planissimum* *Plagusia tuberculata* *Thalamita integra* *Thalamita* sp.
5	Vancouver, Canada	*Hemigrapsus oregonensis*
6	Port Allen Harbor, Kauai, Hawaiian Islands	*Sesarma (erythrodactyla?)*
7	Salt Point State Park, Sonoma County, California	*Pagurus hirsutiusculus*
8	Hookipa Park, Maui, Hawaiian Isl.	unidentified hermit crab
9	Lahaina, Maui, Hawaiian Islands	*Grapsus tenuicrustatus* *Ocypode ceratophtalmus*
10	Coos Bay, Oregon	*Cancer magister* *Cirolana harfordi* *Hemigrapsus oregonensis* *Idotea wosnesenskii*
11	Assateague Island, Maryland	*Cancer irroratus* *Emerita talpoida* *Gammarus* sp. *Limulus polyphemus*
12	San Pedro, California	*Callinectes bellicosus* *Libinia* sp. *Paguristes* sp. *Pleuroncodes planipes* *Sicyonia ingentis*
13	Wailua, Kauai, Hawaiian Islands	*Ocypode ceratophtalmus*
14	Papawei Point, Maui, Hawaiian Isl.	*Ocypode ceratophtalmus*
15	Dinosaur Nat'l. Monument, Colorado	*Locusta migratoria*
16	Lumahai Beach, Kauai, Hawaiian Islands	*Grapsus tenuicrustatus* *Ocypode ceratophtalmus*
17	Anahola Bay, Kauai, Hawaiian Isl.	*Ocypode ceratophtalmus*
18	San Francisco Bay, California	*Artemia franziscana*
19	Mono Lake, California	*Artemia monica*
20	Bodega Bay, California	*Callianassa californiensis* *Hemigrapsus nudus* *Hemigrapsus oregonensis* *Pachygrapsus crassipes* *Petrolisthes cinctipes* *Upogebia pugettensis*
21	Eureka, California	*Hemigrapsus oregonensis* *Pachygrapsus crassipes*
22	Palos Verdes, California	*Pachygrapsus crassipes*

Number	Location	Species sampled
23	Leo Carillo State Beach, Calif.	*Blepharipoda occidentalis* *Cancer antennarius* *Hemigrapsus oregonensis* *Pachygrapsus crassipes* *Panulirus interruptus*
24	Boston, Massachusetts	*Homarus americanus*
25	Howe Sound, Canada	*Hemigrapsus nudus*
26	Seattle, Washington	*Hemigrapsus nudus*
27	Venice, California	*Emerita analoga*
28	San Felipe, Mexico	*Callinectes arcuatus* *Hemigrapsus (nudus?)* *Lophopanopeus (maculatus?)* *Petrolisthes* sp.
29	Manhattan Beach, California	*Emerita analoga*
30	Malibu Lagoon State Beach, Calif.	*Hemigrapsus oregonensis*
31	Ensenada, Mexico	*Pachygrapsus crassipes* *Pugettia producta*
32	Hapuna Beach, Hawaii	*Thalamita* sp.
33	Onekahakaha Beach, Hawaii	*Dardanus insignus*
34	Mahana Bay, Hawaii	*Ocypode ceratophtalmus*
35	Dana Point, California	*Cancer antennarius* *Hemigrapsus oregonensis* *Pachygrapsus crassipes* *Pagurus* sp. *Petrolisthes* sp.
36	Noz-Ramet, river Meuse, Belgium	*Oronectes limosus*
37	Boulogne-sur-Mer, France	*Carcinus maenas*
38	John o'Groat's, Great Britain	*Carcinus maenas* Gammaridea
39	Balmacara, Great Britain	*Carcinus maenas* Gammaridea
40	Liège, Belgium	*Agelostica alni* *Vespula germanica*
41	Antwerpen, Belgium	*Locusta migratoria*
42	Montpellier, France	*Scarabeus laticollis*
43	Duino, Italy	*Eriphia verrucosa* *Ilia nucleus* *Macropodia* sp. *Parthenops* sp. *Squilla* sp. unidentified hermit crabs
44	Rovinj, Yugoslavia	*Ilia nucleus* *Maia (verrucosa?)* unidentified hermit crab
45	Berlin, Germany	*Astacus leptodactylus*
46	Lake Tahoe, California	*Pacifactacus leniusculus* unidentified maggots
47	Joshua Tree Nat'l. Monument, California	*Erythrodiplax funerea*
48	Mayaguana Island, Bahamas	*Callinectes sapidus* *Cardisoma (guanhumi?)* *Grapsus* sp. *Panulirus argus*
49	Capistrano Beach Park, Calif.	*Emerita analoga*
50	Santa Monica State Beach, California	*Emerita analoga*
51	Providenciales Island, Caribbean	*Paguristes* sp.
52	Pacatnamu, Peru	*Callinectes arcuatus* *Euphylax dovii* *Panulirus gracilis* *Pinnotherelia laevigata*
53	Jequetepeque river, Peru	*Macrobrachium inca*
54	Harbor Lake, San Pedro, Calif.	*Procambarus clarkii*
55	Alondra Park, Los Angeles, California	*Procambarus clarkii*
56	Crystal Lake, San Bernardino Mountains, California	*Pacifastacus leniusculus*
57	UCLA Botanical garden, Los Angeles, California	*Procambarus clarkii*
58	Brawley, Imperial County, Calif.	*Procambarus clarkii*
59	Badwater, Death Valley, Calif.	*Hydrophilus (lineata?)* unidentified insect larvae

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A STABLE CARBON ISOTOPE EVALUATION OF THE CONTRIBUTION OF TERRIGINOUS CARBON TO THE MARINE FOOD WEB IN BAYBORO HARBOR, TAMPA BAY, FLORIDA

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ABSTRACT

The isotopic composition of various organic inputs was used to identify the importance of land-derived organics, introduced via runoff, in supporting the food web in Bayboro Harbor, Tampa Bay. Particulate organic carbon, phytoplankton, and representative bivalves, were collected during periods of little or no terrestrial input (dry season, March–May and October–November 1981, January–February and October–December 1982) and during periods of high terrestrial input (rainy season, June–September 1981, March–September 1982, February 1983). Land-derived organic input was composed of two types: plants following the C_3 photosynthetic pathway with a mean of −27.7‰, and grasses following the C_4 photosynthetic pathway with a mean of −12.6‰.

All samples were lighter during periods of high terrestrial input. Phytoplankton, composed primarily of diatoms, was 0.8‰ lighter (−20.4‰ *vs* −21.2‰) during the rainy season, particulate organic carbon was 2.8‰ lighter (−20.1‰ *vs* −22.9‰), and bivalves were 2.2‰ lighter (−20.1‰ *vs* −22.3‰).

Differences in the isotope ratios between periods of high and low terrestrial input could be due to incorporation of land-derived organics into the food web and/or phytoplankton fixation of lighter inorganic carbon.

INTRODUCTION

The mass-induced difference in chemical and physical reactivities of ^{13}C and ^{12}C results in significant variations in stable carbon isotope ratios (expressed using the accepted $\delta^{13}C_{PDB}$ notation) during physical and biological processes. Researchers have repeatedly used $\delta^{13}C$ signatures to study the flow of carbon, *e.g.*, in salt marshes (Smith and Epstein 1970; Haines 1976a,b; Haines and Montague 1979; Hackney and Haines 1980; Hughes and Sherr 1983) in seagrass beds (Thayer, Parker, LaCroix and Fry 1978; Fry and Parker 1979; McConnaughey and McRoy 1979b; McMillan, Parker and Fry 1980; Fry, Scalan and Parker 1983) and in oceanic food webs (Fry *et al.* 1983; Rau, Mearns, Young, Olson, Schafer and Kaplan 1983; Thayer, Govoni and Conally

1983). These uses are based on the observation that different plant food sources have distinctive isotope ratios (Parker 1964; DeNiro and Epstein 1978; Kneib, Stiver and Haines 1980) which are generally preserved throughout the food chain (Tregunna, Smith, Berry and Downton 1970; Bender 1971; Smith and Epstein 1971; Eadie 1972; McConnaughey and McRoy 1979a) although some variations in the different trophic levels have been found (Fry and Parker 1979, McConnaughey and McRoy 1979a, Thayer *et al.* 1983).

Several studies have been conducted in the past few years to determine the importance of land-derived organics in supporting marine food webs (Hackney and Haines 1980, Thayer *et al.* 1983) using the $\delta^{13}C$ dichotomies that have been demonstrated between the C_3 pathway in land plants and marine organic matter (Park and Epstein 1960, 1961; Bender 1968, 1971; Smith and Epstein 1971; Troughton, Card and Hendy 1974; O'Leary 1981). Terrestrial matter introduced via runoff may also be an important carbon source for some marsh invertebrates (Hackney and Haines 1980) though a study of the food web in the northern Gulf of Mexico failed to show any effect of terrestrial organic carbon on the planktonic food web (Thayer *et al.* 1983). On the other hand, Stephenson and Lyon (1982) and Incze, Mayer, Sherr and Macko (1982) found a gradation from heavier to lighter values in bivalves as up-river distances increased.

This study was undertaken in Bayboro Harbor, Tampa Bay, Florida (Fig. 1) to determine if land-derived organic carbon is being incorporated into the marine food web. Bayboro Harbor has two sources of organic matter; terrestrial organic matter introduced via runoff and marine organic matter synthesized by algae. Three stations were occupied in the study area. Station I, well within the Harbor receives fresh water input from general land runoff and point source contributions from Salt Creek and Booker Creek, whereas Station III, close to the opening into Tampa Bay, receives only the former. There was no statistical difference between the $\delta^{13}C$ values from these two stations (95% confidence limit, student's *t* test) so the results from each were pooled as one. Station II is located in Salt Creek and is generally quite fresh, although there are periodic infusions of salt water during high tides.

MATERIALS AND METHODS

Phytoplankton, particulate organic carbon (POC) and oysters were collected during March–November 1981, January–February 1982, and January–February 1983 at various sites around Bayboro Harbor.

Phytoplankton was collected by towing a 63 μm mesh size net. After collection, all samples were stored in glass vials and jars and refrigerated. Particulate organic carbon (POC) was collected by filtering water samples through a pre-combusted Whatman GF-C glass fiber filter. Prior to combustion, samples were treated with 2N HCl to remove any carbonate carbon present, and dried at 50° C for 24–48 hrs. The method used to combust the sample is described by Sofer (1980) and a device similar to that described by DesMarais and Hayes (1976) was used for cracking the pyrex tubes.

Most samples contained nitrogen oxides which interfered with the CO_2 signal when introduced into the mass spectrometer. These oxides were initially removed by adding mercury to the sample bulbs and allowing the mercury to react as follows at room temperature:

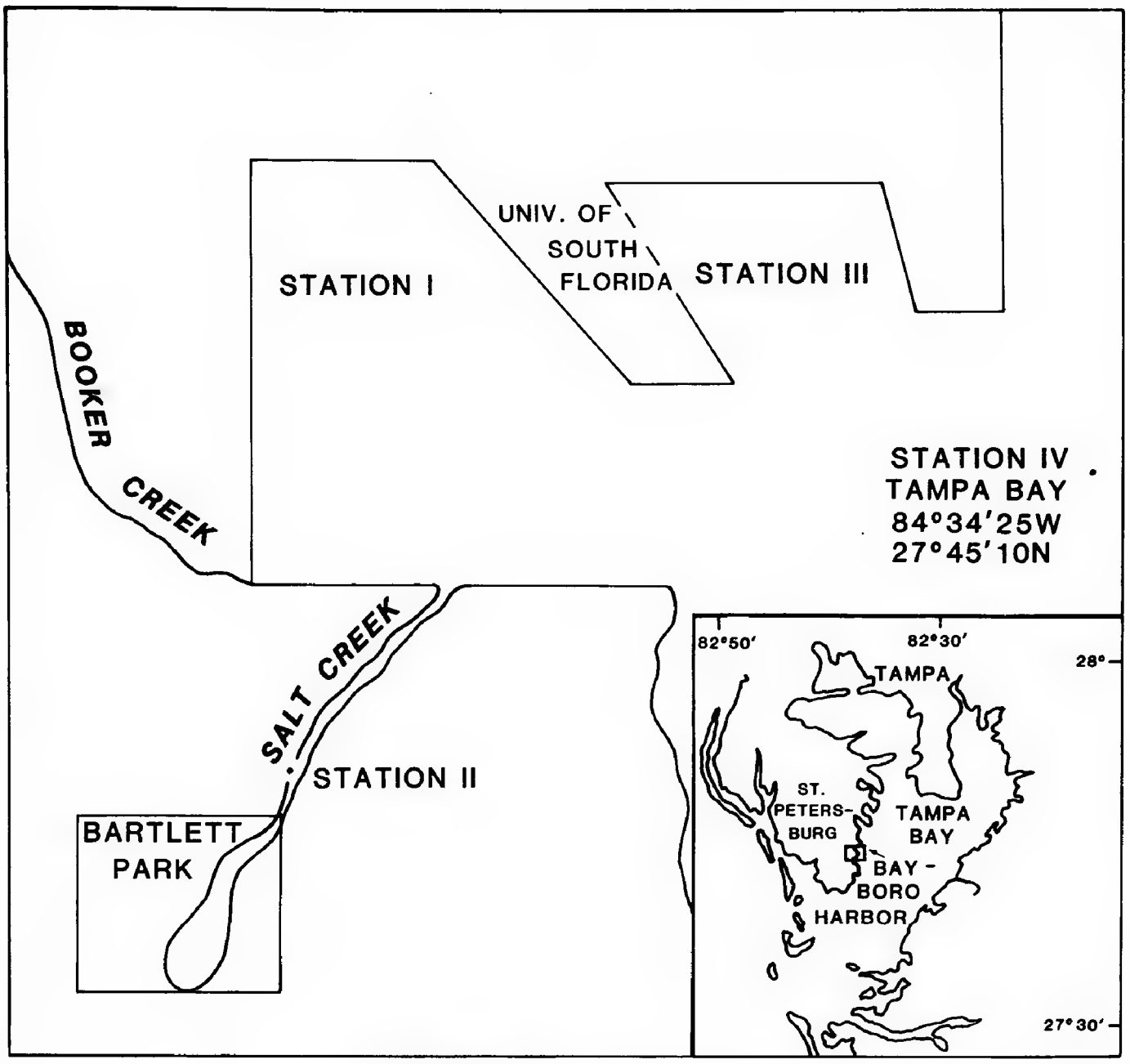

FIG. 1. Location of sampling stations in Bayboro Harbor, St. Petersburg, Florida.

$$(Hg + N_xO_y \leftarrow HgO + N_2).$$

The N_2 was then pumped away after freezing out the CO_2 with liquid nitrogen. An alternate method, used in some cases, was to transfer the impure CO_2 to another ampoule containing copper metal and reacting for 2 hours at 500° C

$$(N_xO_y + Cu \leftarrow N_2 + CuO).$$

Dissolved inorganic carbon was determined by the standard method of reacting 85% phosphoric acid with the pre-filtered water sample. Salinities were determined using an Autosal model 8400 from Guideline.

The isotopic composition of carbon is expressed using the del notation:

$$\Delta\,{}^{13}C = (R_{sample}/R_{standard} - 1) \times 1000$$

where $R = {}^{13}C/{}^{12}C$ and results are expressed as parts per thousand difference from the PDB standard.

$\delta^{13}C$ values were determined in a triple collector Finnigan Mat 250 Isotope Ratio Mass Spectrometer relative to a charcoal working standard ($\delta^{13}C = -24.8‰$ *vs.* PDB) for organic matter and relative to a Solenhofen limestone standard ($\delta^{13}C = -0.15‰$ *vs.* PDB) for inorganic samples.

Figure 2 shows the monthly rainfall for the 2½ year period covered by this study. For the period defined as the dry season (March–May and October–November 1981, January–February and October–December 1982 and January 1983) the cumulative amount was 44.40 cm; for the period defined as the rainy season (June–September and December 1981, March–October 1982 and February 1983) the cumulative amount was 282.68 cm.

RESULTS AND DISCUSSION

Table 1 compares the data obtained for samples collected during the wet season with those collected during the dry season. $\delta^{13}C$ values were lighter for the rainy season with the mean values more negative during the wet season by 0.8‰ for phytoplankton, 2.8‰ and 3.0‰ for POC in Bayboro Harbor and Salt Creek respectively, and 2.2‰ for bivalves in Bayboro Harbor. Even though these differences are within natural variations of the populations, they are

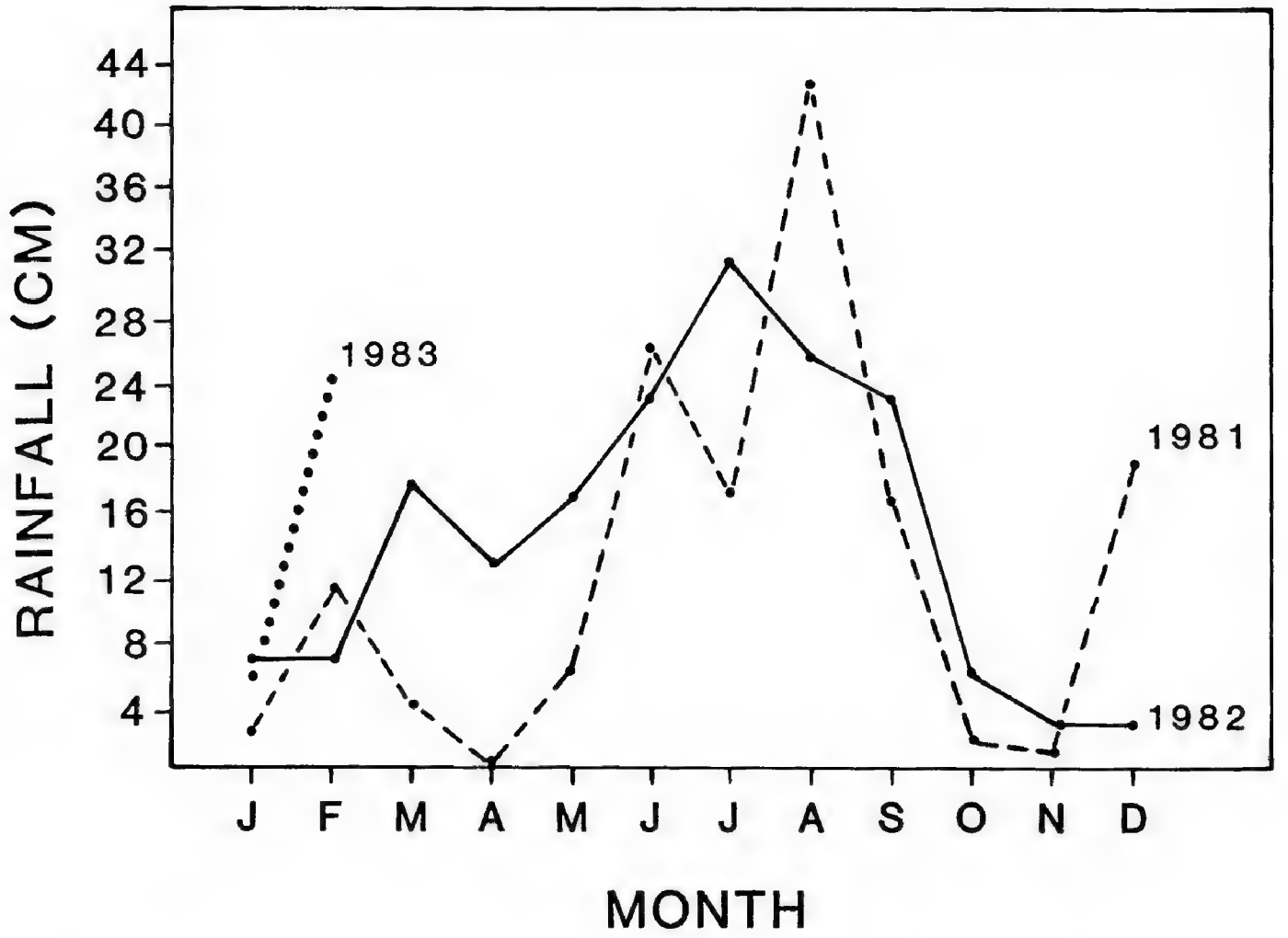

FIG. 2. Rainfall (cm/month) in St. Petersburg, Florida, March 1981–February 1983.

TABLE 1

Data for samples collected during the dry and rainy season.

Sample	Dry Season $(\delta^{13}C^{o}/oo)_{PDB}$				Rainy Season $(\delta^{13}C^{o}/oo)_{PDB}$			
	n	Range	Mean	Std. Dev.	n	Range	Mean	Std. Dev.
Phytoplankton (Bayboro)	7	-20.1 to -20.8	-20.4	0.2	6	-21.0 to -21.3	-21.2	0.2
POC (Bayboro)	7	-19.6 to -21.0	-20.1	0.6	7	-22.2 to -23.2	-22.9	0.4
POC (Salt Creek)	4	-18.9 to -21.9	-20.2	1.4	6	-22.6 to -24.0	-23.2	0.5
Oyster, *Crassostrea virginica*	5	-19.6 to -21.0	-20.1	0.6	5	-21.7 to -22.7	-22.3	0.4

consistently found for all the samples. The systematic differences in $\delta^{13}C$ values found for phytoplankton, POC and bivalves collected during the dry and rainy season could be due to:

1) Changes in the plankton species composition
2) Changes in the $\delta^{13}C$ values of dissolved inorganic carbon (DIC), which would change phytoplankton and its predator compositions
3) Incorporation of different terrestrial carbon sources
4) Selective herbivory by bivalves.

Changes in Phytoplankton Composition

Numerous studies have shown phytoplankton carbon isotope ratios to be dependent on the species composition of the sample (Sackett, Eadie and Exner 1974; Fontugne and Duplessy 1978; Wong and Sackett 1978; Rau, Sweeney and Kaplan 1982; Gearing and Gearing 1983). In this study, the major phytoplankton present throughout the year were identified to determine if changes in species composition were the cause for any changes in the $\delta^{13}C$ values of the phytoplankton. However, little or negligible variations in the species composition were found. Diatoms and blue-greens predominated year round in Bayboro Harbor. The dominant diatoms are *Skeletonema costatum, Coscinodiscus* spp., *Nitzschia* spp., *Rhizosolenia* spp. and *Chaetoceros* spp. Although dinoflagellates, particularly *Gonyaulux* and *Ceratium,* have been reported to be quite dominant in Tampa Bay (Turner and Hopkins 1974) they were not apparent in any of the samples that were analyzed. This may have been due to loss of smaller species during filtration of samples.

Several blue-green algal blooms occurred throughout the study (May and July 1981, and February 1982 and 1983 both dry and rainy season), therefore any affect on the $\delta^{13}C$ values of the phytoplankton populations would be taken into account during both seasons.

Variation in ^{13}C of Dissolved Inorganic Carbon

Mixing of fresh and light water with heavier marine waters will result in changes in the $\delta^{13}C$ values for dissolved inorganic carbon (DIC) (Sackett and Moore 1966, Spiker and Schemel 1979, Sherr 1982, Tan and Strain 1983). For example, Sackett and Moore (1966) found a $\delta^{13}C$ DIC gradient with distance from shore associated with a salinity gradient. Riverine DIC with $\delta^{13}C$ values of -8‰ were shown to mix with oceanic DIC with $\delta^{13}C$ values of 0‰. In the case of Bayboro Harbor, a salinity range of 10‰ is found with the lowest being 20‰ during the rainy season.

Five DIC samples analyzed for Station II (Salt Creek), three from Station I and one from Station III showed a positive correlation ($r = +0.96$) between salinity and $\delta^{13}C$ DIC. The heaviest sample, and most saline, was collected in the river during high tide. The range of $\delta^{13}C$ DIC collected during the dry season was -1.5 to -4.4‰. Three samples collected during the rainy season had $\delta^{13}C$ values of -2.0, -4.9 and -6.6‰ (salinities were extrapolated for two of these values). As salinities range between 20–30‰ in the harbor, the $\delta^{13}C$ DIC would range between -1.0 to -3.5‰. If phytoplankton are fixing the lighter DIC entering the harbor, they would become up to 2.5‰ lighter than open Tampa Bay samples. This process probably accounts for negative shifts in phytoplankton $\delta^{13}C$ values found following input of riverine water into the harbor.

Terrestrial Plant Contribution

A survey was made of the common vascular plants surrounding Salt Creek and Bayboro Harbor. Plant specimens were collected along Bartlett Park situated at the head of Salt Creek (Fig. 1), and from litter found in the phytoplankton nets. Four C_4 grasses, *Paspalum* spp. (Bahia grass), *Cynodon dactylon* (Bermuda grass), *Stenotaphrum secundatum* (St. Augustine grass) and *Digitaria sanguinalis* (crab grass) had a narrow $\delta^{13}C$ range of -11.6‰ to -13.7‰ with a mean -12.6‰, which is in agreement with the data given by Bender (1971), Smith and Epstein (1971), and others.

Nine different C_3 plants showed a much wider range, -25.4‰ to -31.7‰ with a mean -27.7‰. All samples except *Sabal palmetto* (Cabbage palm), *Laguncularia racemosa* (white mangrove) and one *Quercus laurifolia* (laurel oak) were leaf litter found floating in the harbor. A 0.8‰ difference was measured between the leaf of a laurel oak collected along the river, and the leaves found floating in the river. This is within the variability between species of the same plant, 0.8 to 3.0‰, reported by Fry (1977), and thus cannot be related to changes induced by decomposition.

Equal contributions of C_3 and C_4 plants into the harbor would cause the $\delta^{13}C$ values of terrestrial carbon input to become heavier and approach plankton compositions. This would nullify the use of carbon isotopes as a tracer in the Bayboro Harbor marine food web. However, on the basis of land plant debris identified in net tows, C_3 plants predominate.

Particulate Organic Carbon Composition

Particulate organic carbon (POC) collected in Bayboro Harbor during the dry season was −20.1‰ and was comprised predominantly of phytoplankton. During the rainy season, the average POC value was 2.8‰ lighter, apparently reflecting an increased input of terrestrial organic carbon and a shift in phytoplankton values induced by lighter terrestrial inorganic carbon. The lighter values could also be due to blooms of smaller plankton during the rainy season. Gearing, Gearing, Rudnick, Requejo and Hutchins (1984) reported lighter values for nannoplankton than for larger phytoplankton species. A shift in the plankton composition would be evident in the POC fraction which includes both large and small phytoplankton. A dominance of plankton carbon during this period was still evident since the POC values were much closer to mean phytoplankton values (−21.2‰) than to mean terrestrial carbon (−27.7‰) values. The range in isotope values for all the POC samples collected was large (0.8 to 1.5‰) which is indicative of heterogeneity of the POC.

POC was also sampled in the river (Salt Creek) (Fig. 1 and Table 1) and a 3.0‰ difference between seasons was found. $\delta^{13}C$ POC results for dry periods (x = −20.2‰, range −18.9 to −21.9‰) were only 0.1‰ lighter than the mean POC found in the harbor, suggesting a plankton dominance in the river. During the rainy season, POC samples had mean values of −23.2‰ (range −22.6‰ to −24.0‰). It appears that about 1/3 of the −3‰ shift is due to the change in $\delta^{13}C_{DIC}$ and 2/3 to the contribution of terrestrial plant debris.

Bivalves

Oyster samples, *(Crassostrea virginica)*, show a 2.2‰ difference between rainy (−22.3‰) and dry (−20.1‰) seasons. Oysters were lighter than phytoplankton (−21.2‰) and heavier than POC (−22.9‰) during the rainy season (Table 1). During the dry season, this enrichment between bivalves and the POC fraction was not evident. The results indicate that bivalves are either utilizing both phytoplankton and terrestrial carbon and/or selectively feeding on smaller plankton species during the rainy season.

CONCLUSIONS

In Bayboro Harbor of Tampa Bay, Florida, USA mean $\delta^{13}C$ values for samples of phytoplankton, particulate organic carbon and oysters show a negative shift of 0.8, 1.8 and 2.2‰, respectively. The phytoplankton shift is apparently due to the negative $\delta^{13}C$ change for dissolved inorganic carbon values induced by freshwater inputs whereas the change in particulate organic carbon and oysters $\delta^{13}C$ values are, in large part, due to the contribution of land plant debris, a component of POC and the food stuff of oysters and/or a shift in the dominance of smaller phytoplankton during the rainy season.

LITERATURE CITED

BENDER. M.M. 1968. Mass spectrometric studies of carbon 13 variations in corn and other grasses. *Radiocarbon.* **10**:468–472.

_____. 1971. Variations in the $^{13}C/^{12}C$ ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry.* **10**:1239–1244.

DeNIRO, M.J. and S. EPSTEIN. 1978. Influence of diet on distribution of carbon isotopes in animals. *Geochimica Cosmochimica Acta.* **42**:495–506.

DesMARAIS, D.J. and J.M. HAYES. 1976. Tubecracker for opening glass-sealed ampoules under vacuum. *Analytical Chemistry.* **48**:1651–1652.

EADIE, B.J. 1972. Distribution and fractionation of stable carbon isotopes in the Antarctic ecosystem. Ph.D. Dissertation. Texas A&M University. 118pp.

FONTUGNE, M. and J.C. DUPLESSY. 1978. Carbon isotope ratio of marine plankton related to surface water masses. *Earth and Planetary Science Letters.* **41**:365–371.

FRY, B.D. 1977. Stable carbon isotope ratios — a tool for tracing food chains. M.S. Thesis. University of Texas, Austin. 125 pp.

_____ and P.L. PARKER. 1979. Animal diet in Texas seagrass meadows: ^{13}C evidence for the importance of benthic plants. *Estuarine and Coastal Marine Science.* **8(6)**:499–509.

_____, R.S. SCALAN AND P.L. PARKER. 1983. $^{13}C/^{12}C$ ratios in marine food webs of the Torres Strait, Australia. *Australian Journal of Marine Freshwater Research.* **34**:700–715.

GEARING, J.N., P.J. GEARING, D.T. RUDNICK, A.G. REQUEJO and M.J. HUTCHINS. 1984. Isotopic variability of organic carbon in a phytoplankton based, temperate estuary. *Geochimica Cosmochimica Acta.* **48**:1089–1098.

GEARING, P.J., and J.N. GEARING. 1983. Variability in carbon isotopes of plankton and underlying estuarine benthos. Abstract. *Estuaries.* **6(3)**:303–304.

HACKNEY, C.T. and E.B. HAINES. 1980. Stable carbon isotope composition of fauna and organic matter collected in a Mississippi estuary. *Estuarine and Coastal Marine Science.* **10**:703–708.

HAINES, E.B. 1976a. Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt marsh. *Estuarine and Coastal Marine Science.* **4**:609–616.

_____. 1976b. Relation between the stable carbon isotope composition of fiddler crabs, plants, and soils in a salt marsh. *Limnology and Oceanography.* **21**:880–883.

_____ and C.L. MONTAGUE. 1979. Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. *Ecology.* **60(1)**:48–56.

HUGHES, E.H. and E.B. SHERR. 1983. Subtidal food webs in a Georgia estuary: ^{13}C analysis. *Journal of Experimental Marine Biology and Ecology.* **67**: 227–242.

INCZE, L.S., L.M. MAYER, E.B. SHERR, and S.A. MACKO. 1982. Carbon inputs to bivalve mollusks: a comparison of two estuaries. *Canadian Journal of Fisheries and Aquatic Science.* **39**:1348–1352.

KNEIB, R.T., A.E. STIVER and E.B. HAINES. 1980. Stable carbon isotope ratios in *Fundulus heteroclitus* (L.) muscle and gut contents from a North Carolina *Spartina* marsh. *Journal of Experimental Marine Biology and Ecology.* **46**:89–98.

McCONNAUGHEY, T. and C.P. McROY. 1979a. ^{13}C label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. *Marine Biology.* **53**:263–269.

_____. 1979b. Food web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology.* **53**:257–262.

McMILLAN, C., P.L. PARKER and B. FRY. 1980. $^{13}C/^{12}C$ ratios in seagrasses. *Aquatic Botany.* **9**:237–249.

O'LEARY, M.H. 1981. Carbon isotope fractionation in plants. *Phytochemistry.* **20(4)**:553–567.

PARK, R. and S. EPSTEIN. 1960. Carbon isotope fractionation during photosynthesis. *Geochimica Cosmochimica Acta.* **21**:110–126.

_____. 1961. Metabolic fractionation of C^{13} and C^{12} in plants. *Plant Physiology.* **36**:133–138.

PARKER, P.L. 1964. The biogeochemistry of the stable isotopes of carbon in a marine bay. *Geochimica Cosmochimica Acta.* **28**:1155–1164.

RAU, G.H., A.J. MEARNS, D.R. YOUNG, R.J. OLSON, H.A. SCHAFER and I.R. KAPLAN. 1983. Animal $^{13}C/^{12}C$ correlates with trophic levels in pelagic food webs. *Ecology.* **64(5)**:1314–1318.

_____, R.E. SWEENEY and I.R. KAPLAN. 1982. Plankton $^{13}C/^{12}C$ change with latitude: differences between northern and southern oceans. *Deep-Sea Research.* **29**:1035–1039.

SACKETT, W.M., B.J. EADIE and M.E. EXNER. 1974. Stable isotope composition of organic carbon in Recent Antarctic sediments. In *Advances in Organic Geochemistry.* France.

_____ and W.S. MOORE. 1966. Isotopic variations of dissolved inorganic carbon. *Chemical Geology.* **1**:323–328.

SHERR, E.B. 1982. Carbon isotope composition of organic seston and sediments in a Georgia salt marsh estuary. *Geochimica Cosmochimica Acta.* **46**:1227–1232.

SMITH, B.N. AND S. EPSTEIN. 1970. Biochemistry of the stable isotopes of hydrogen and carbon in salt marsh biota. *Plant Physiology.* **46**:738.

_____. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. *Plant Physiology.* **47**:380–384.

SOFER, ZU. 1980. Preparation of carbon dioxide for stable carbon isotope analysis of petroleum fractions. *Analytical Chemistry.* **52(8)**:1389–1391.

SPIKER, E.C. and L.E. SCHEMEL. 1979. Distribution of stable isotope composition of carbon in San Francisco Bay. pp. 195–212. In T.J. Conomos (ed.) *San Francisco Bay: the Urbanized Estuary.* Pacific Division, AAAS, San Francisco.

STEPHENSON, R.L. and G.L. LYON. 1982. Carbon-13 depletion in an estuarine bivalve: detection of marine and terrestrial food sources. *Oecologia.* **55**:110–113.

TAN, F.C. and P.M. STRAIN. 1983. Sources, sinks, and distribution of organic carbon in the St. Lawrence Estuary, Canada. *Geochimica Cosmochimica Acta.* **47**:125–132.

THAYER, G.W., J.J. GOVONI and D.W. CONALLY. 1983. Stable carbon isotope ratios of the planktonic food web in the northern Gulf of Mexico. *Bulletin of Marine Science.* **33(2)**:247–256.

_____, P.L. PARKER, M.W. LaCROIX and B. FRY. 1978. The stable carbon isotope ratio of some components of an eelgrass *Zostera marina* bed. *Oecologia.* (Berlin) **35**:1–12.

TREGUNNA, E.B., B..N. SMITH, J.A. BERRY and W.J.S. DOWNTON. 1970. Some methods for studying the photosynthetic taxonomy of the angiosperms. *Canadian Journal of Botany.* **48**:1209–1214.

TROUGHTON, J.H., K.A. CARD, and C.H. HENDY. 1974. Photosynthetic pathways and carbon isotope discrimination by plants. *Carnegie Institute of Washington Yearbook.* **73**:768–780.

TURNER, J.T. and T.L. HOPKINS. 1974. Phytoplankton of the Tampa Bay system, Florida. *Bulletin of Marine Science.* **24(1)**:101–121.

WONG, W.W. and W.M. SACKETT. 1978. Fractionation of stable carbon isotopes by marine phytoplankton. *Geochimica Cosmochimica Acta.* **42**:1809–1815.

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ANALYSIS OF BIOLOGICAL AND CHEMICAL ASSOCIATIONS NEAR A TURBID COASTAL FRONT DURING WINTER 1982

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ABSTRACT

An intense front separates the waters of the nearshore region from those of the Louisiana inner shelf. Horizontal salinity gradients often exceed 0.25‰ km^{-1} Data from hydrographic cruises and moored instruments are used to characterize the variability in and around the front during winter/spring, when the structure is most changeable. A modified empirical orthogonal function analysis explains 88% of the data variability with three basic patterns: 1) high nitrate and silicate concentrations are strongly associated with the low-salinity nearshore waters; 2) an association between high chlorophyll *a* concentration and low temperature reflects, we believe, both parameters' relationship with turbid shallow depths rather than a direct interaction; 3) coincidental high ammonia and zooplankton concentrations are, presumably, due to excretion. In contrast to oceanic fronts, these shelf fronts do not lead to regional boundary zones of increased biologic activity.

INTRODUCTION

Perhaps the most characteristic feature of the west Louisiana continental shelf is the presence of two localized sources of intense freshwater discharge: the Mississippi and Atchafalaya river deltas. Near these sources, the river plumes strongly influence the physics (Wiseman, Murray, Bane and Tubman 1982), the chemistry (Ho and Barrett 1975), and the biology (Hanson 1982) of the shelf waters. Farther downstream of the deltas, this runoff contributes to a low-salinity, highly turbid nearshore region (Crout 1983; Kelly, Schmitz,

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Randall and Cochrane 1983a). Even during low runoff conditions, the nearshore waters may be 5 to 10‰ fresher than the inner-shelf waters. Furthermore, the front separating the nearshore, low-salinity waters from the inner-shelf waters is very sharp [$0(0.25‰\ km^{-1})$]. Much weaker fronts are known to be the sites of significant biological and chemical associations in other coastal regions of the world (*e.g.*, Holligan 1981). However, strong coastal fronts near major rivers have not received much attention.

During the winter of 1982, two data sets were separately collected over the inner shelf near the Texas-Louisiana border (Kelly, Cochrane, Randall and Schmitz 1983b; Continental Shelf Working Group 1982). In this paper, these data are reanalyzed to determine whether biological and chemical associations occurring at weak frontal boundaries also occur at the intense front separating the west Louisiana nearshore waters from the adjacent inner-shelf waters.

The working hypothesis we test here with descriptive and statistical analyses is: Phytoplankton are light limited in the shallow, turbid coastal boundary layer and nutrient limited seaward, where zooplankton biomass is higher owing to exploitation of increased food resources.

MATERIALS AND METHODS

The first data set was collected during four monthly cruises: January to April 1982. These occupied the grid shown in Fig. 1. The easternmost line of stations was occasionally abbreviated because of bad weather. Temperature and salinity profiles were obtained at each station using a Guildline Model 8770 CSTD, which was calibrated both in a controlled bath and against field samples. The system operated within the manufacturer's stated accuracy of ±0.04‰ and ±0.02° C. Water samples for chemical analyses were collected with teflon-lined 2.5L Niskin bottles. Unfiltered samples were placed in autoanalyzer vials, frozen on board, and analyzed on land for ammonia, silicate, nitrate, and phosphate concentrations using a Technicon Autoanalyzer AAII. Between 500 and 1000 ml aliquots were filtered through cellulose acetate filters (0.45 μ nominal pore size) to determine chlorophyll *a* concentration. Chlorophyll *a* was extracted with acetone and measured spectrophotometrically with a correction for phaeopigments (Strickland and Parsons 1968).

Zooplankton were collected using 60-cm opening and closing 335-micron mesh nets. Ten-minute stepped oblique tows were made at a speed of about 1 m/s. The net was rinsed with seawater and the sample preserved in 10% formalin. Samples were later transferred to 5% formalin. After removal of nonplanktonic organisms, *e.g.*, seaweed and large fish, zooplankton biomass was measured both as dry weight and displacement volume. Since zooplankton dry weight was positively correlated with displacement volume ($R^2 > 0.85$), only the dry-weight data will be discussed below.

The second data set was collected by one or two Endeco 174 current meters moored at each of the three sites indicated on Fig. 1. Calibration procedures are described elsewhere (Kelly, Olsen, Schmitz and Ulm 1983c). The data from these moorings were low-pass filtered with a symmetric Lanczos filter having a 2-hr half-power point and subsampled at 0.5-hr intervals to eliminate sampling noise and high-frequency turbulence. These were further low-pass filtered with a 40-hr half-power point to eliminate the tidal frequencies.

RESULTS

The bathymetry in the study area is relatively smooth, apart from a discontinuous ridge, which is less than 5 m deep. Local runoff is derived from

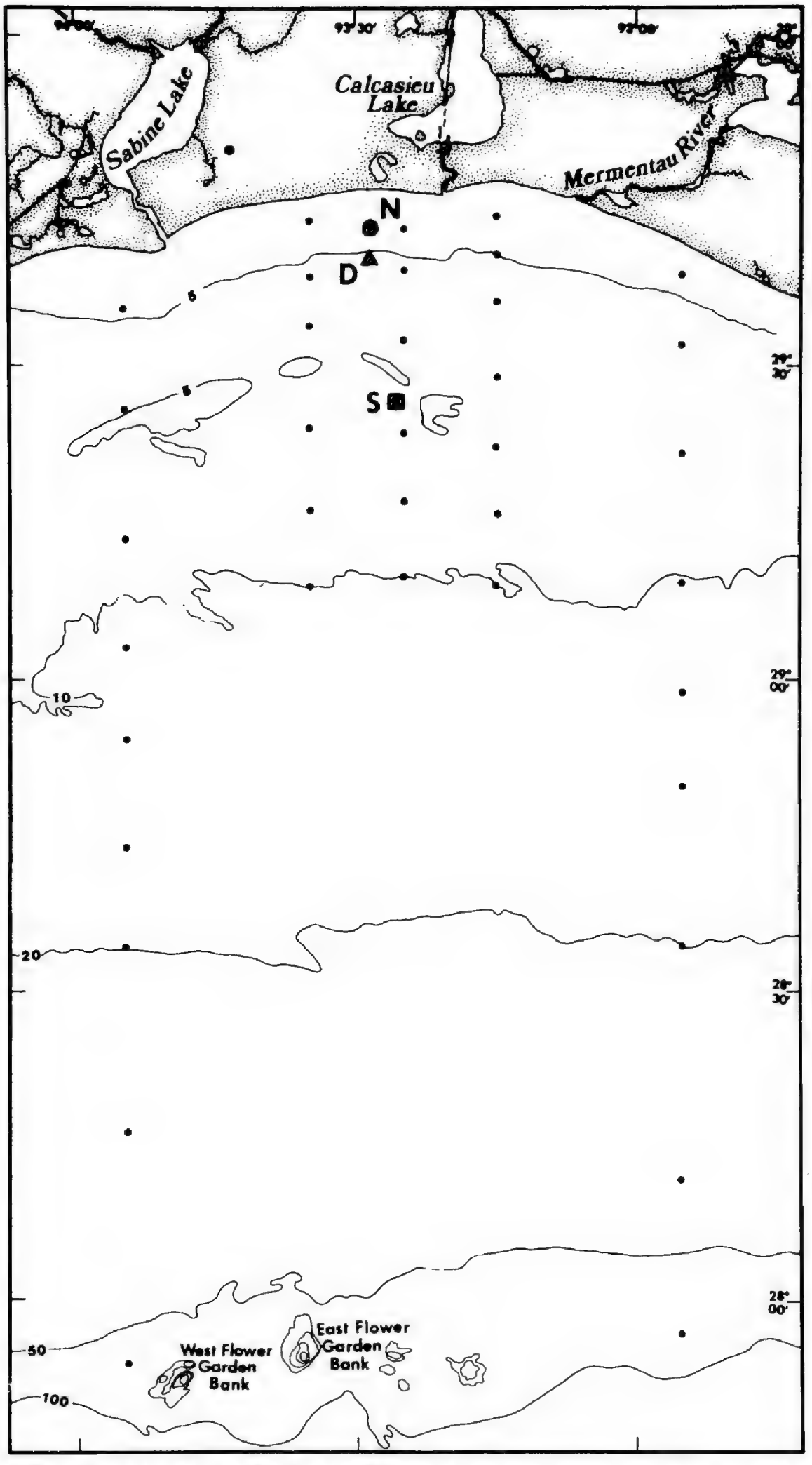

FIG. 1. Location chart showing the grid of hydrographic stations (small dots) and the three current meter sites (S, D, and N). Depth contours are in meters.

three estuaries (from west to east): Sabine Pass, Calcasieu Pass, and the Mermentau River. However, the greatest volume of fresh water delivered to the region originates 175 km to the east at the Atchafalaya River delta. In 1982, discharge from the Atchafalaya River exhibited a broad flood period, with three periods of peak runoff (Kelly *et al.* 1983a). Discharge began to rise in late January and remained high until mid-March, when a dip occurred followed by a second peak in early April. Flow declined through late May, when it then rose to a final peak in late June.

Inner-shelf and nearshore water density gradients are essentially controlled by salinity, not temperature, in this region. Temperature effects on the absolute value of density are important on the annual time scale, though. Examples of the salinity structure are shown in Fig. 2. Although the cross-shelf salinity gradients are strong over most of the inner shelf, the most intense front is located within 10 to 20 km of shore. The March data are the exception (see below). The surface maps suggest topographic steering of the nearshore waters by Sabine Bank. (Note the approach of the isohalines toward the coast in the vicinity of Calcasieu Pass.) The vertical structure of the water column is variable. During our cruises we observed weak vertical stratification in January, February, and April. During the winter, the northern Gulf of Mexico is influenced by severe cold fronts passing over the shelf every 3 to 10 days (Fernandez-Partegas and Mooers 1975). The strong associated mechanical mixing vertically homogenizes the water column. Later in the season, as the storms become weaker and less frequent and river discharge increases, the structure reverses, on time scales of the order of a week,

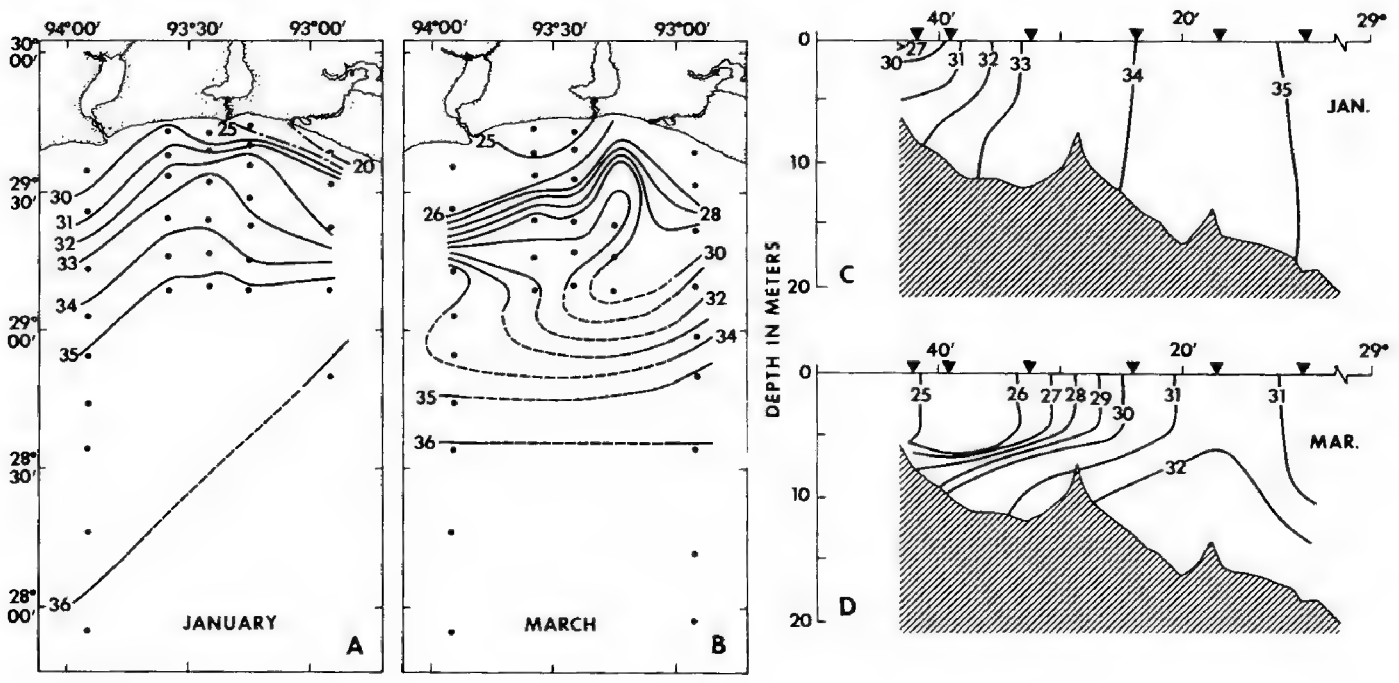

FIG. 2. A) Surface salinity pattern for cruise of January 18–21, 1982. (Note the change in salinity contour interval for salinities less than 30‰.)
B) Surface salinity pattern for cruise of March 7–10, 1982.
C) Salinity section along 93° 25′ W during January 1982 cruise.
D) Salinity section along 93° 25′ W during March 1982 cruise.

between nearly vertically well mixed and two-layered conditions (*e.g.*, our March cruise).

The response of the nearshore and inner-shelf currents to the frontal passages is seen in Fig. 3, which presents stick plots of the low-pass filtered winds and currents from the study period. Shallow-water wind-driven currents along the Louisiana shelf during winter appear to be strongly controlled by frictional effects and bathymetry (Chuang and Wiseman 1983, Crout 1983). (Baroclinic effects increase in importance as wind forcing diminishes in late spring.) Since the front separating the inner-shelf and nearshore waters lies well within this shallow-water region, the currents measured at all three mooring sites were extremely similar. No strong shear was observed across the frontal boundary, although there was a tendency for increased levels of onshore-offshore variability at the seaward station, suggesting less coastal constraint (Csanady 1981) at this site. During the summer, though, when winds are weaker and a strong vertical stratification develops, a significant vertical and cross-shelf shear is evident (Crout 1983). This situation may also

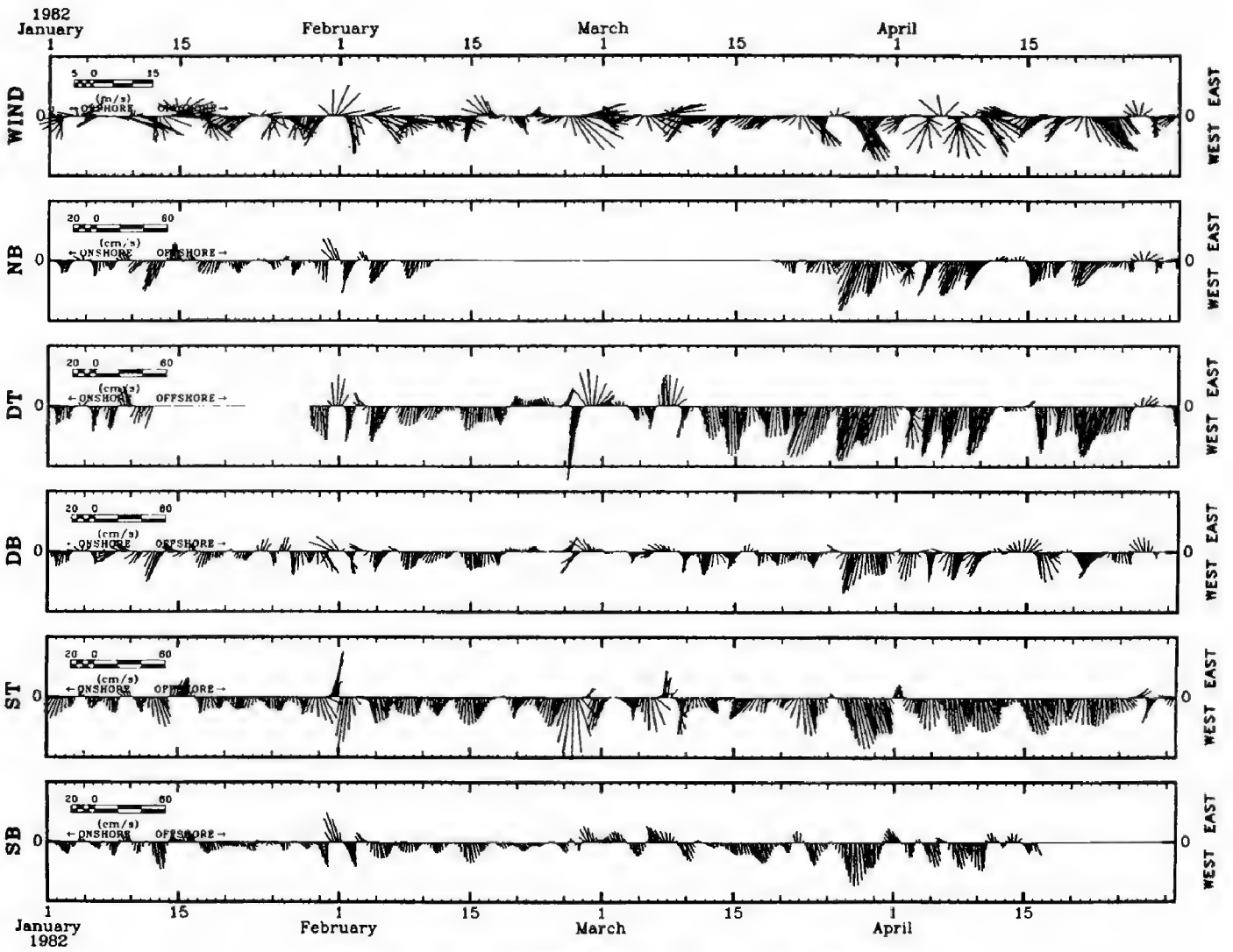

FIG. 3. Stick plots of the 40-hr low-pass-filtered winds and currents during the study period. Meters DT and ST were moored 4 m below the sea surface. Meters NB, DB and SB were moored 2 m above the bottom.

occur during two-layered stratified conditions such as our March data. (Note the shear between DT and DB and between DT and ST from late February through at least mid-March.)

The mean flow at all stations was westward and nearly parallel to shore, as would be expected in a wind-driven coastal boundary layer. (Steering by local bathymetry, though, may be important during isolated periods, *viz.* Fig. 2B, Fig. 3.) Furthermore, the eddy fluxes of salt (calculated from half-hour samples of the 2-hr low-passed records from the current meters) in both the cross-shelf and alongshelf directions were less than 4% and 7% of the respective mean advective fluxes in all records except one. During March/April, the cross-shelf turbulent flux of salt in the surface layer at Station S (Fig. 1) was of the same magnitude as the cross-shelf mean advective flux.

Tides in this region are moderate to weak. The current meter records show no influence directly attributable to the exchange with Calcasieu Pass. The inability of tidal mixing to homogenize the summer water column attests to the role of winter wind mixing in maintaining the vertical winter frontal boundary.

Examples of the surface distributions of nitrate, ammonia, silicate, and chlorophyll *a* are presented in Fig. 4. These patterns are far more patchy than the patterns of salinity. They often show an onshore-offshore gradient. The regions of greatest structure, though, appear to lie somewhat seaward of the salinity front. The ammonia distribution consistently shows a region of low ammonia seaward of the salinity front.

The zooplankton dry weights ranged from 1 to 50 mg/m^3 during the study. There were relative highs near shore and near mid-shelf. These distributions, too, though, are extremely patchy (Continental Shelf Working Group 1982).

Interpretation

The present data were used to examine the following three hypotheses.

(1) The nearshore waters of Louisiana are extremely turbid owing to both resuspension and sediment introduction with the river runoff. Secchi disc depths in the coastal boundary layer east of the Atchafalaya River are commonly less than 1 m (Sklar and Turner 1981), and satellite photographs of sediment plumes indicate more sediment being added as the coastal boundary layer mixes with the Atchafalaya River effluent and flows into the study area (O.K. Huh, personal communication). Phytoplankton within this region are light limited. Unpublished bioassay experiments with nutrient additions and deletions and light regime management have documented this (Turner, in preparation). Furthermore, light saturation of the phytoplankton in the turbid coastal waters to the east usually occurs only in the top 10 cm (Sklar and Turner 1981).

(2) Immediately offshore of the salinity front separating the nearshore waters from the inner-shelf waters (~20–30 km from shore), turbidity drops and the phytoplankton community is effectively nutrient-limited, yet still

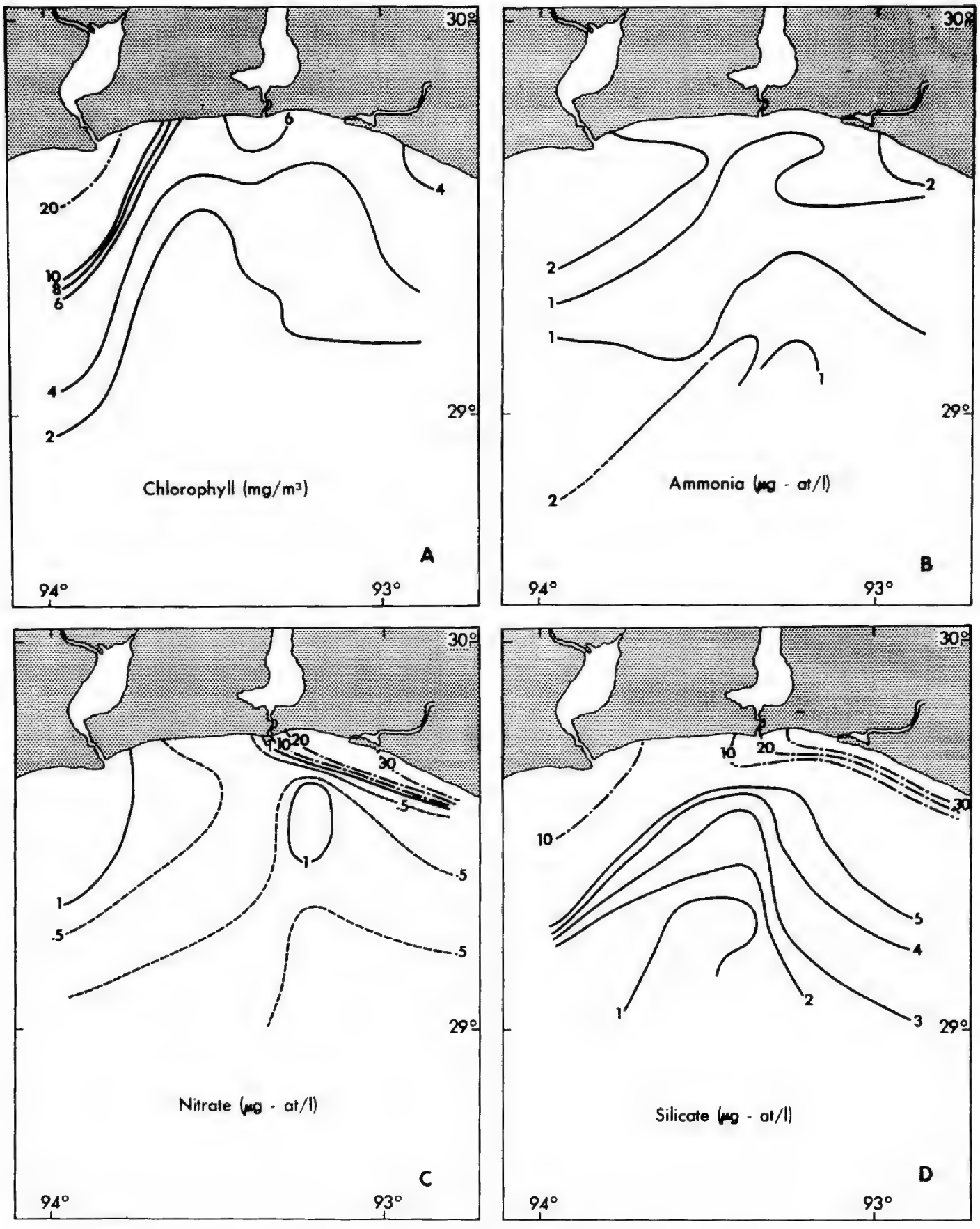

FIG. 4. Surface nutrient distributions during the cruise of January 18–21, 1982.
A) Chlorophyll *a*,
B) Ammonia,
C) Nitrate and
D) Silicate.

highly productive. Pigment concentrations per cell are anticipated to be lower offshore, in the better light conditions (Parsons and Takahashi 1973).

(3) Immediately seaward of this zone of high phytoplankton activity, the populations of zooplankton are highest, because of the increased phytoplankton food source.

In order to qualitatively test these hypotheses, we decided to objectively look for patterns in the distribution data. To do this, we utilized a modified empirical orthogonal function analysis (Overland and Priesendorfer 1982). The technique quantitatively estimates orthogonal patterns in a data set. These patterns may be interpretable in terms of reasonable ecological models.

Two analyses were run. First, we analyzed the surface data for relationships among the following parameters: temperature, salinity, nitrate, ammonia, silicate, and chlorophyll *a*. In the second analysis, we vertically averaged each of the aforementioned data sets and combined it with the available zooplankton data, for the three cruises during which the waters were relatively well mixed (vertically).

When the surface patterns were analyzed, the dominant association, which accounted for 43.5% of the total normalized variability, was between low salinities and high values of silicate and nitrate. This suggests nutrient introduction with the river runoff and conservative mixing on the shelf, particularly the inner shelf. The second most important pattern was an association of low temperatures with high chlorophyll *a* concentrations. During the winter season, the lowest temperatures on the shelf are associated with the shallow, turbid nearshore waters. We believe that this second pattern, in reality, is expressing a direct association between high chlorophyll *a* and turbidity. This is because the plankton within the turbid nearshore waters are expected to compensate for lower light levels by increasing the concentration of chlorophyll *a* per cell. In later vertically averaged analyses, when depth was substituted for temperature in the parameter string, essentially the same pattern emerged, with depth playing the same role as temperature. A summer data set, when temperature and depth are inversely related, is required to definitively test this idea. The third most important pattern showed ammonia to be varying essentially independently of the other parameters.

When the vertically averaged data were analyzed, similar patterns emerged. The dominant association was (P1, Fig. 5), once again, between low-salinity waters and high concentrations of silicate and nitrate. The second most important pattern (P2, Fig. 5) associated low temperature and zooplankton concentration with high chlorophyll *a* and ammonia concentrations. Again, we believe that temperature is acting as a surrogate for depth. The inverse relationship between zooplankton and ammonia concentrations in P2 suggests that the ammonia is being flushed from the marshes rather than excreted locally by zooplankton. Marshes can be net exporters of nitrogen (Nixon 1980), and Barataria Bay (to the east of the study region) exhibits higher levels of ammonia in the Bay than in the nearshore waters (Ho and Barrett 1975). Finally, the third most important pattern (P3, Fig. 5) shows

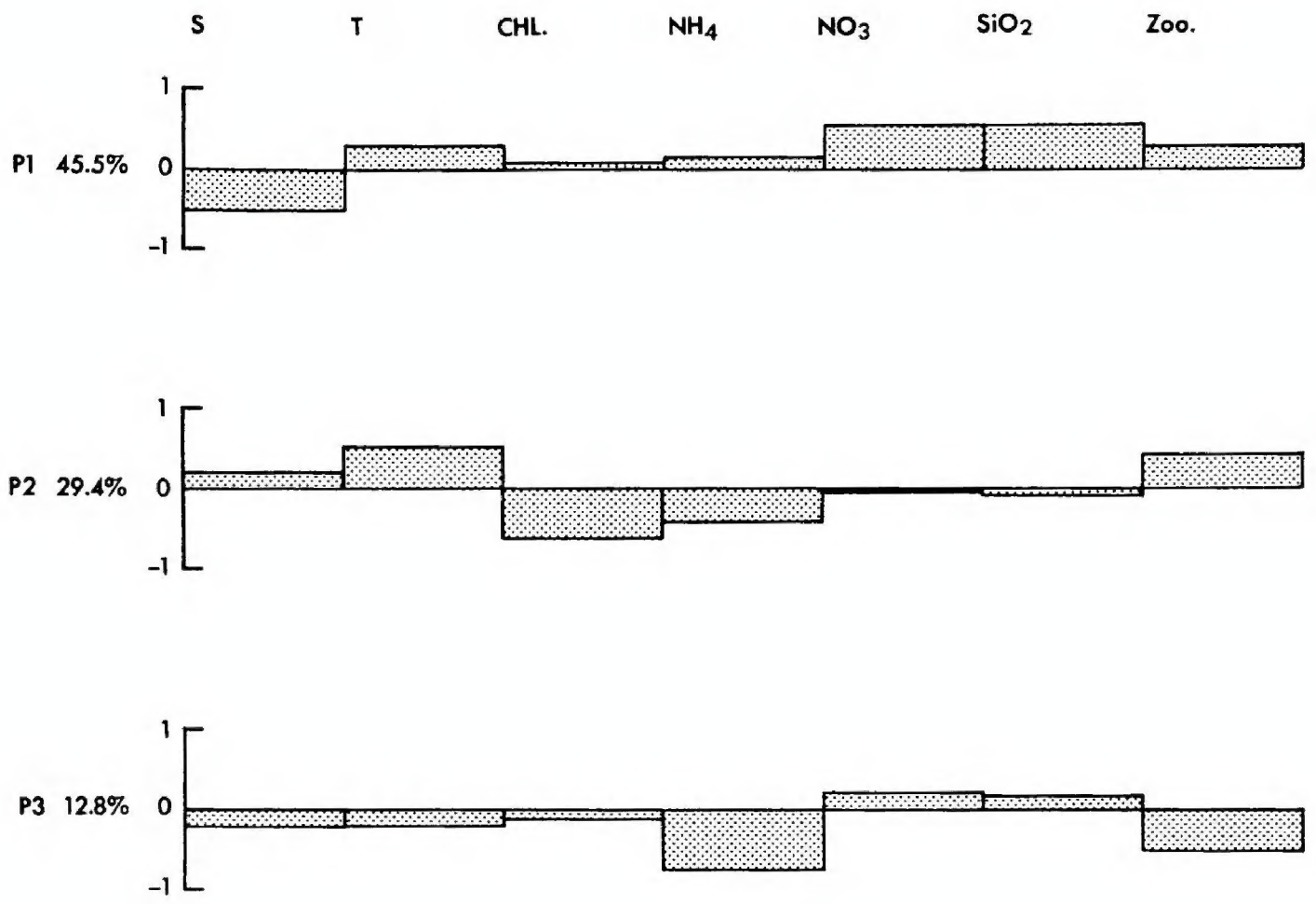

FIG. 5. The three most important patterns, P1, P2 and P3, determined by the empirical orthogonal function analysis, for the vertically averaged data from the January, February and April cruises. The percentage of the total variability in the data explained by each pattern is also shown.

a strong positive association between ammonia and zooplankton, indicating excretion of ammonia by zooplankton.

The most significant differences between the results of the analysis and our original hypothesis are: (1) there is no evidence of nutrient utilization by the growing phytoplankton to an extent that any one nutrient is being obviously depleted and (2) the low ammonia concentrations found outside the salinity front do not appear to be an anomaly caused by ammonia utilization. Rather, the high ammonia concentrations farther offshore (over the mid-shelf area) appear to be an addition resulting from zooplankton excretion.

DISCUSSION

Elsewhere in the world, coastal fronts prevent mixing and retain phytoplankton in the photic zone, where they rapidly reproduce, generating high local chlorophyll *a* concentrations and stripping nutrients from the water column. Holligan (1981) describes such a situation at the Ushant front off the Brittany coast of France. In this case tidal mixing maintains the frontal boundary, whereas along the Louisiana coast winter wind mixing is a main energy source maintaining the front. In these other regions, biological

processes modified by the frontal dynamics appear to be controlling the chemical distributions in the regions where the horizontal density gradients are strongest. Along the Louisiana coast, in contrast, an individual phytoplankton cell is kept in an effective photic zone because the water is so shallow and mixing so intense that it cannot get deep enough and remain long enough to be in a region where its primary productivity is precluded. Within the most intense frontal region and shoreward of this zone, runoff, marsh/estuary export, and dispersion appear to be the dominant controls on the chemical distributions. Seaward of the region of maximum horizontal density gradient, chlorophyll *a* concentrations are altered as the phytoplankton adjust to improved light conditions in the less turbid waters. Only over the mid-shelf regions do we see apparent biological control of the chemical species in a region where the ammonia concentrations seem to increase dramatically.

These conclusions are based on the analysis of data from cruises that were not initially designed to study frontal properties. The data spacing is somewhat coarse. The signals are so strong, though, that our interpretation of the data, at least on the largest spatial and temporal scales, appears valid. Clearly, finer scale studies still have the potential for modifying these conclusions.

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LITERATURE CITED

CHUANG, WEN-SSN AND W.J. WISEMAN, JR. 1983. Coastal sea level response to frontal passages on the Louisiana-Texas shelf. *Journal of Geophysical Research.* **88(C4)**: 2615–2620.

CONTINENTAL SHELF WORKING GROUP. 1982. *Evaluation of the Brine Disposal from the West Hackberry Site: The Regional Impact on Menhaden Resources.* Vols. I and II. Center for Wetland Resources, Louisiana State University, Baton Rouge.

CROUT, R.L. 1983. Wind-driven, near-bottom currents over the west Louisiana inner continental shelf. Ph.D. dissertation, Louisiana State University, Baton Rouge, 117 p.

CSANADY, G.T. 1981. Circulation in the coastal ocean. *Advances in Geophysics.* **23**:101–183.

FERNANDEZ-PARTEGAS, J. and C.N.K. MOOERS. 1975. A subsynoptic study of winter cold fronts in Florida. *Monthly Weather Review.* **103**:742–744.

HANSON, R.B. 1982. Influence of the Mississippi River on the spatial distribution of microheterotrophic activity in the Gulf of Mexico. *Contributions in Marine Science.* **25**:181–198.

HO, CLARA and B.B. BARRETT. 1975. Distribution of nutrients in Louisiana's coastal waters influenced by the Mississippi River. *Technical Bulletin. Louisiana Wildlife and Fisheries Commission, Oysters, Wetland Bottoms and Seafoods Division.* No. **17**.

HOLLIGAN, P.M. 1981. Biological implications of fronts on the northwest European continental shelf. *Philosophical Transactions of Royal Society of London.* **A302**:547–562.

KELLY, F.J., J.E. SCHMITZ, R.E. RANDALL and J.D. COCHRANE. 1983a. Physical oceanography. In R.W. Hann, Jr. and R.E. Randall (eds.) Evaluation of Brine Disposal from the Bryan Mound Site of the Strategic Petroleum Reserve Program: Annual Report for September 1981 through August 1982. Chapter 1. Department of Energy. Available from NTIS, Springfield, Va., DOE/P010114–5.

————, J.C. COCHRANE, R.E. RANDALL and J.E. SCHMITZ. 1983b. Physical oceanography. In L.R. DeRouen, R.W. Hann, Jr., D.M. Casserly and C.P. Giammona (eds.) West Hackberry Strategic Petroleum Reserve Brine Site Brine Disposal Monitoring, Year I Report, Final Report. Chapter 2. Department of Energy. Contract DE-AC96-80P010288.

————, Y.E. OLSEN, J.E. SCHMITZ, and W.F. ULM. 1983c. Physical oceanography. In L.R. DeRouen, R.W. Hann, Jr., C.P. Giammona and R.E. Randall (eds.). Strategic Petrolem Reserve Brine Studies in the Gulf of Mexico, Field and Laboratory Procedures Manual. Chapter 5. Department of Energy. Available from NTIS, Springfield, VA. DOE/P010850-1.

NIXON, S.W. 1980. Between coastal marshes and coastal waters—a review of 20 years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. pp. 437–525. In P. Hamilton and K.B. MacDonald (eds.) *Estuarine and Wetland Processes,* Plenum, New York.

OVERLAND, J.E. and R.W. PRIESENDORFER. 1982. A significance test for principal components applied to a cyclone climatology. *Monthly Weather Review.* **110(1)**:1–4.

PARSONS, T. and M. TAKAHASHI. 1973. *Biological Oceanographic Processes.* Pergamon, Oxford, 186 pp.

SKLAR, F.H. and R.E. TURNER. 1981. Characteristics of phytoplankton production off Barataria Bay in an area influenced by the Mississippi River. *Contributions in Marine Science.* **24**:93–106.

STRICKLAND, J.D.H. and T.R. PARSONS. 1968. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada.* **167**:85–206.

WISEMAN, W.J., JR., S.P. MURRAY, J.M. BANE and M.W. TUBMAN. 1982. Temperature and salinity variability within the Louisiana Bight. *Contributions in Marine Science.* **25**:109–120.